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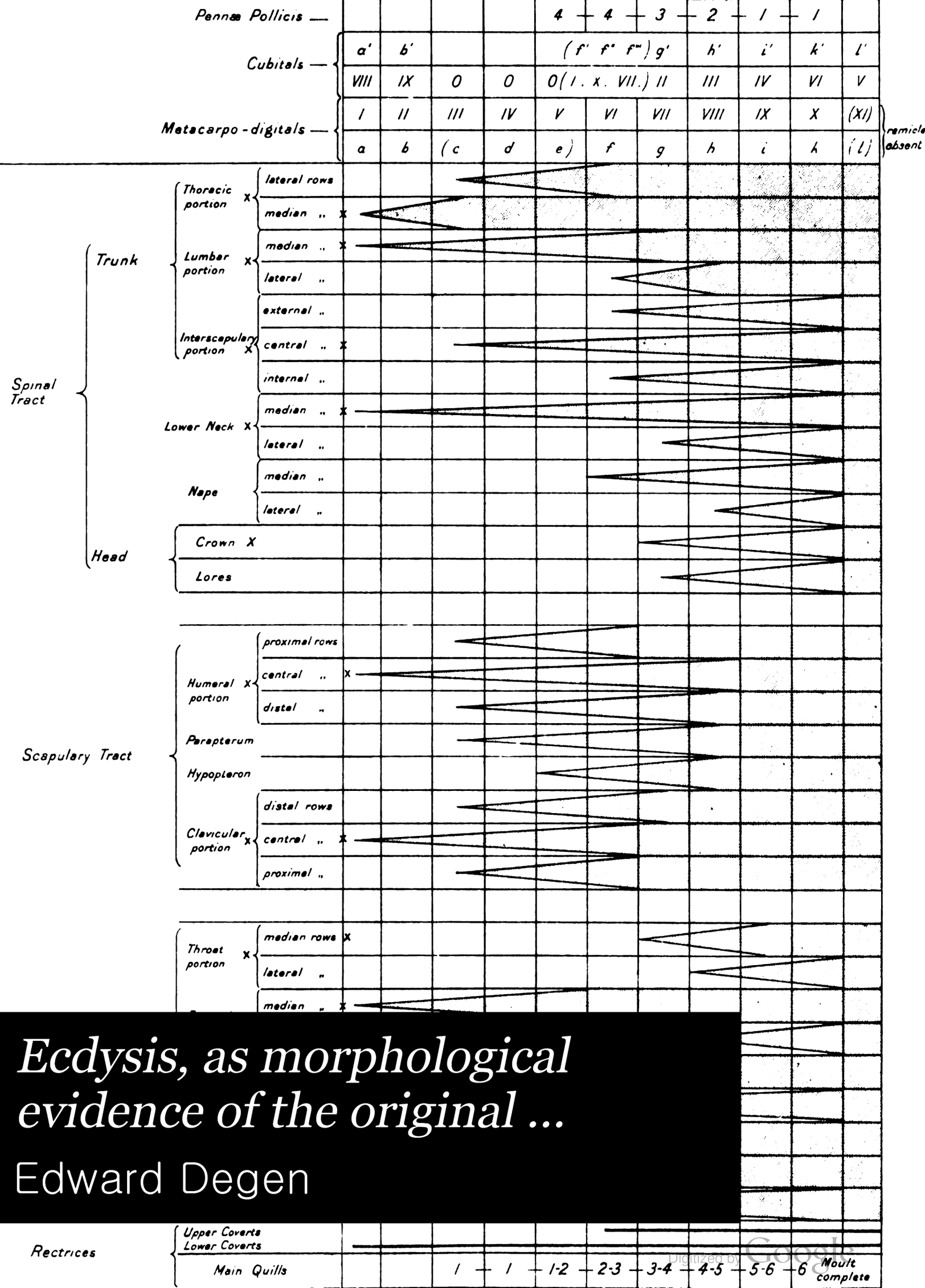

Ecdysis, as morphological evidence of the original ...

Edward Degen

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Continued on page 3 of Wrapper.

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IX. *Ecdysis, as Morphological Evidence of the Original Tetradactyle Feathering of the Bird's Fore-limb, based especially on the Perennial Moult in* Gymnorhina tibicen.

By EDWARD DEGEN, *F.Z.S.*

Received October 16, 1901; read February 4, 1902.

[Plates XXXVI.–XXXVIII.]

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I.—INTRODUCTORY.

THE main object of this paper is to give additional evidence in support of the theory of the derivation of the feathering of the bird's wing.

When I was engaged on the subject of Diastataxy (Aquinto-cubitalism), the peculiar conditions of the flight-feathers during the moult seemed to indicate that, by a fuller study of the perennial moult, the facts concerning the observations of the feathers of the bird's wing might be considerably elucidated.

In order, then, to form a solid foundation for the purely morphogenetic development of the feathers, it was necessary to ascertain the mode by which the perennial moult of the individuals of a species of bird is made up, from the earliest to the last stages of renewal; and, further, to what extent each feather participates in this annual

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process during the period of complete feather-change. This has been methodically treated and fully explained in the present paper.

By a "feather-change" there can be meant one thing only, namely, the actual renewal of all the feathers.

Physical changes, arising from external agencies, such as colour-changes, or the abrasion of the wing-coverts and contour-feathers of the body, with their attendant effects upon the pattern of the plumage, do not enter into the scope of this work. Neither do partial changes, such as spring-plumages and the various forms of nuptial garbs, of a sexual nature; nor do the phenomena of "Albinism" and "Melanism," all these being either of a secondary origin, or, as in the latter case, of an ætiological nature.

II.—Historical.

With regard to the literature, it may be well to review in a general way those papers which deal with the morphological history of the feathers. For a more exhaustive account of the history of the "moult," I refer the reader to the excellent article of Dr. Allen (1), who has considered previous authors chronologically, and at the same time has himself contributed to the physiology of the subject.

By far the most important addition to the subject of "moult" was that made by Blyth (4) in 1837, who, amongst other observations relative to colour-changes, makes remarks on the plumage of birds which are of great value. Among many excellent attributes characterizing his work, is that of a comparatively far advanced pterylographic knowledge before the time of appearance of the classic treatise of Nitzsch's 'Pterylography,' edited by Burmeister, and first published in 1840 (Translation, 37)[1].

Blyth's work is replete with information, based principally on the "Mallard" and the "Widgeon"; but though he bestowed much care on the partial and perennial moult of the primaries and the tail-feathers, he treated but scantily the wing-coverts. To this author's paper I have made frequent reference in the course of my own research.

Schlegel's famous "Address" (40) gave a new impetus to the subject of ecdysis. I shall have to allude more particularly in the course of my own work to the various

[1] Yarrell's endeavour to adduce evidence in favour of his view, "*that the feather itself becomes altered*"[a]—though in the course of his arguments he admits "that it is certainly difficult to understand how this is so constantly effected in the web of the feather, *where no vascularity can be shown to exist*[a], even when the part is growing" (*cf.* Allen, *l. c.*),—is shared also by Blyth to a great extent. Burmeister's observations and researches into the histological structure of the feather (see Nitzsch, *l. c.*), and also Holland (29), should, however, finally dispel any doubts still existing on the point of a revitalization of the feather.

[a] These *italics* are mine.

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statements made by this author under the different chapters. Allen has criticized it in a general way.

Amongst the principal dissentients from the laws formulated by Schlegel respecting the season, manner, degrees, and methods of moult and alleged changes of colour without moult, should be mentioned, as the foremost, Homeyer, who in 'Rhea,' ii. 1846, p. 157, published some remarks; he also replied to Schlegel in a communication to 'Naumannia' (1853), and further by numerous comments on this subject (see Bibliography, 30, 30 *a*, 31).

To the most prolific writers of that period who subjected the seasonal and other changes to a fuller scrutiny, unquestionably belongs Brehm (6, 7, 8, 9, & 10) by reason of a large amount of material gathered for this purpose by his son Alfred. However, apart from the profusion of *a priori* argument and some other additional information, his inquiries had to a great extent the object of refuting the "thesis" laid down by Schlegel, and also similar views held by Martin (32, 33).

Important contributions to the knowledge of the chemico-physical changes in the feather-structure itself were those of Altum (2), Meves (34), and Bogdanow. Meanwhile the question gave rise to a number of minor contributions, consisting of critical remarks or casual observations on the subject, such as those of Gloger (24, 25, 26), Hesler (28), Böck (5), Dwight (18), v. Müller (36), Gätke (22), Cabanis, and many others.

Until the appearance of the translation from the Swedish of Sundevall's work (43), a great deal of confusion existed in regard to a scientific knowledge of the topography of the feathering in birds. Sundevall has done much to remedy this deficiency, and confined his researches largely to this character, though principally to the serial values, of the feathers on the wing.

It is from this point that the researches conducted into the derivation of the plumage began in earnest, as Nitzsch's 'Pterylography,' which appeared in 1840, seems to have been little known or appreciated by his own countrymen, and it was not until the able translation into English, published in 1867 by Dr. P. L. Sclater for the Ray Society, was available that its worth became generally recognized. And in reading Nitzsch, it is not a little remarkable to find that the portion dealing with the covert-feathers on the wing should have received so little attention. Nevertheless, it is to the last-named authors, Sundevall and Nitzsch (37), that we are primarily indebted for a beginning of the study of the morphological question concerning the feathering of the wings of birds.

After this, with the exception of two short papers in 1856 by Dr. Weinland—one in Journ. f. Ornith. iv. pp. 125–129, and the other in Proc. Boston Soc. Nat. Hist. iv. (1856–59) pp. 34–37,—a period of calm set in, which was broken only by the important work published in 1866 by Dr. Fatio (19), who had meantime conducted a series of investigations into the changes of the plumage, both chemico-physical and physiological. To this memoir I have been frequently indebted.

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After Fatio's publication, the subject again lapsed, when it was reopened in 1877 with a short contribution by Gerbe (23). To this author we are indebted for the first allusions made to the genetic relations of the flight-feathers and their coverts. Gerbe refers the student, at the beginning of his paper (which seems to have been merely intended as a preliminary article), to some subsequent and more comprehensive account of this subject. This appears never to have been published. This author's researches do not extend beyond the flight-feathers and their principal coverts, as may be seen on p. 290, *l. c.*, pars. 9 & 10.

The next important memoir which appeared is that of Dr. Gadow (20), which throws much light upon the physical and chemical aspect of the feather-structure.

Ignoring for the present a number of casual and disjointed observations which have found their way into literature during this interval, we must look for the next really important contribution towards a more orderly knowledge of the conditions determinating the process of moult in birds to that made in 1896 by Dr. Wittmer Stone (44).

Apart, however, from the prominent part which this author has allotted to the main quills and other feather-tracts of the body, the object of his researches principally centres in an elucidation of the relationship of the moult with the seasonal changes of the plumage in as great a number of families, genera, and species of the birds of North America as possible.

With the exception of the entries made on table iii., p. 116, of his work on the relative condition of the smaller land-birds, no information is given about the covert-feathers. To this work I have had to refer repeatedly in my arguments concerning the different parts of the plumage.

Soon after this there appeared in rapid succession articles by John Guille Millais (35), "On the Change of Birds to Spring-Plumage without a Moult" (referring to the Grebe and Dunlin, but principally the Sanderling), and that by Dr. Chapman (13), also on the Dunlin, the Sanderling, and the Snowflake.

In another paper in 1897, this latter author (15) also made some remarks in reply to Dr. Chadbourne's (11) exhaustive account of his observations on the "Spring Plumage of the Bobolink." The last-quoted papers have mostly dealt with the question of colour-change with or without moult.

Works with a more direct bearing upon the morphological features of the wings of birds, and especially their coverts, are those of Goodchild (27), Wray (46), Gadow (21), and Pycraft (38). More recently, again, Chalmers Mitchell (12) and Pycraft (39) have made attempts to arrive at a final solution of the question of Diastataxy. In these two papers, which appeared contemporaneously, the interest attaching to the wing-coverts as the most important factors was accordingly renewed, and is proportionate in amount to the different standpoint taken up by these two last-named authors.

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III.—Method of Research.

The practice commonly adopted for the study of the moult is that of observing the changes on birds living in captivity.

Confinement in cages and enclosures, however, as is well known, so greatly alters the natural habits of birds that the information derived from this source is of too uncertain a character to yield reliable results.

As an instance of this contention, I have to mention only the frequent occurrence of the adoption of the plumage of the male by old female birds deprived of the opportunity of pairing. On this point Dr. Fatio (19) makes the following statement (p. 269, *l. c.*):—"Moreover, anyone may have remarked that a bird which has been kept in captivity, or which has been partially deprived of the normal influences acting from without, never attains the perfection of its plumage so completely as the individual which is in a state of freedom" (translation).

Besides, there is abundant evidence for suspecting moult to be affected in those species of birds which are of migratory habits. It is imperative, therefore, to take into consideration the geographical range of such species when inquiring into the subject. To show that this is the case with imported birds, I may quote the following instances which came under my own observation:—

A two-year old *Cacatua roseicapilla* was transferred from Australia to London during the months of October and November. It had just previous to departure entered upon its regular annual moult, in accordance with conditions existing there; this continued during the voyage, and the process was finished at the end of January, which is the normal course for this species. About the month of June, in the same year, this bird, in accordance with the alternating season, entered upon another complete moult, which it terminated in October following, thus undergoing two complete moults (inclusive of flight- and tail-feathers each time) within one calendar year, a totally unnatural proceeding.

The other bird, a six-year old Parrot (*Platycercus eximius*), whose regular period of annual moult in its native habitat is somewhat later, falling within the months of December to March, on account of the wintry conditions prevailing here after its arrival from Australia, suppressed this yearly process altogether till December of the *following year*, which is the month corresponding with the regular conditions for this moult in the southern hemisphere. Its plumage, on account of having been retained for the two consecutive years, was consequently the worse for wear. (See also Böck (5), p. 207, with remark by Dr. Cabanis.)

From these incidents we derive the further information that the latter and older bird adhered to the moulting-season prevailing for the Southern, whilst the former and younger bird, immediately upon transfer, adopted that of the Northern Hemisphere.

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Thus, the comparatively slight discrepancies which must necessarily accrue from the adoption of the theoretical, yet more serviceable, equivalents to those of the empirical figures of their actual measurements, can exert no serious influence on the general result of this investigation.

IV.—Explanatory Remarks on the Diagrams on Plates, Tables, and Charts.

From the 27 specimens more generally described, it seemed advisable to make a narrower selection of 12 typical cases for the purpose of diagrammatic reproductions which illustrate the relative stages of that particular phase which each remex pursues during the moult.

In the diagrams allotted to them in Plates XXXVI.–XXXVIII., these specimens have received a special mark in the shape of a Roman capital letter, irrespective of their serial numbers, which latter are those associated with the dates on which they were received. With these the capital letters correspond tolerably well for denoting the successive stages which are marked by a small Latin letter. The reason for this is that some birds commence to moult sooner than others, and in consequence accomplish the moult earlier. For instance, specimen No. 16, marked F (see Plate XXXVII.), of Dec. 19, which repeats stage *g*, precedes No. 14, of Dec. 11, which is marked G (Plate XXXVII.), because this latter specimen has attained the stage of *h*, which represents the growth of remex VIII. at an earlier date. A similar case to the one mentioned is that of No. 24, and further marked M, of Feb. 18 (Plate XXXVIII.), which had to be placed at the end for representing stage *l'*, or the development of cubital V., as the last remex to appear, because it is a more typical specimen in this respect than No. 25, in which the moult of the same quill has been seemingly accomplished though not entered. Otherwise it bears the same date as the latter specimen—a circumstance which is purely accidental, on account of their having been shot together. Both of these, therefore, antedate No. 26, marked L (Plate XXXVIII.), this having been procured on March 4, which represents the stages intermediate between *i* and *k*, which are earlier than that of No. 24, as we have seen.

Many of these specimens being more or less a repetition only of those extracted for diagrammatical representation, or calling for no special remarks, are referred to only in a general way. Their quotients for the relative lengths of remiges in moult are, however, entered, together with those specially selected for illustration, separately in the two parts of Table I.: part *a* for the left and part *b* for the right wing (see pp. 356–359).

The capital letters which the specimens received in Table I., parts *a* and *b*, correspond with those of the diagrams in Plates XXXVI.–XXXVIII. The specimens are arranged in Table I. in the order of the dates on which they were received. The Roman figures placed at the head of the columns specify the order of the remiges for

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both the metacarpo-digital and the cubital portions of the wing. The column of cyphers to the right contains the sums total of the amount of all the flight-feathers under moult in each specimen. The cyphers placed at the bottom of the columns are the sums total obtained for each remex itself, their aggregates agreeing with the grand total of the other column in the right-hand corner.

The cyphers on the second line at the bottom show the number of specimens observed for the moult of that particular remex, and beneath these, in opposition to the numerical order of figures of the remiges at the top, are placed the letters referring to the successive phases (*cf.* also diagrams on Plates XXXVI.–XXXVIII.), in alphabetical order, for the remiges of the hand portion. Their corresponding equivalents for the order of the cubitals are designated by dashes, thus: ′ ″ ‴.

The symbol O signifies that the remex has been shed, and the dotted spaces are the places still occupied by the old quills.

As already mentioned, a Table has also been provided for the percentages of reduction of power of flight, giving the amount in each specimen, and for each portion of the wing separately, the totals for each wing, and the grand totals for both sides.

V.—Definition of the "Moult."

A. *On "Adventitious Plumage."*

Before a bird assumes the deciduous plumage which is annually replaced in the same manner, viz., by the process known as the "perennial moult," it is provisionally clothed with generally one, though often two liveries, differing both in function and growth. They require careful consideration on account of their genetic importance. The successive liveries are:—

1. An adventitious downy investment of the nestling, or "Embryo-Plumage."
2. A non-deciduous (ontogenetic) garb of the fledgling, or "Annual Plumage."
3. A deciduous (phylogenetic) feathering of the mature bird, or "Perennial Plumage."

It is to the second livery that usually the term "embryo-plumage" is given, chiefly because it produces the first set of quills and contour-feathers (*Teleoptiles*).

In the nestling of *dasypœdic birds* a downy covering (*Neossoptiles*) of the body precedes the latter or plumage of the fledgling. The term "embryo-plumage" therefore belongs to this downy adventitious covering: *cf.* Wittmer Stone (44), pp. 115–117, "Number and Times of Moult"; also Fatio (19), p. 258. These down-feathers are the forerunners of the true contour- and covert-feathers, whose places the latter afterwards occupy. They must therefore not be confounded with the downy structures which grow in the interstices between the latter, such as are found in Ducks, Swans, &c.

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TABLE I. *a*.—Showing the relative lengths of growth

LEFT

METACARPO-DIGITALS.

Date.	No. & Age.	Sex.	X.	IX.	VIII.	VII.	VI.	V.	IV.	III.	II.	I.
A. Nov. 5 ..	1, ad.	♂	..	..	..	..	..	..	..	0	73	81
„ 5 ..	2, juv.	♂	..	..	..	..	..	19	62	83	100	100
B. „ 14 ..	3, juv.	♀	..	..	..	..	..	13	50	80	100	100
„ 14 ..	4, juv.	♂	..	..	..	..	..	..	11	40	66	70
„ 14 ..	5, juv.	♀	..	..	..	..	23	71	100	100	100	100
„ 19 ..	6, juv.	♂	..	..	..	..	0	65	100	100	100	100
C. „ 19 ..	7, ad.	♂	..	..	..	..	4	90	100	100	100	100
„ 19 ..	8, juv.	♂	..	..	..	..	69	100	100	100	100	100
„ 28 ..	9, ad.	♂	..	..	..	..	..	54	91	100	100	100
D. „ 28 ..	10, ad.	♂	..	..	..	9	71	100	100	100	100	100
E. Dec. 3 ..	11, juv.	♀	..	..	..	0	58	100	100	100	100	100
„ 3 ..	12, juv.	♀	..	..	..	..	60	100	100	100	100	100
„ 11 ..	13, juv.	♀	..	..	..	..	51	100	100	100	100	100
G. „ 11 ..	14, juv.	♀	..	0	2	56	100	100	100	100	100	100
„ 19 ..	15, juv.	♂	..	..	..	19	15	100	100	100	100	100
F. „ 19 ..	16, juv.	♂	..	..	..	48	94	100	100	100	100	100
H. Jan. 1 ..	17, ad.	♂	..	..	33	73	58	100	100	100	100	100
„ 1 ..	18, ad.	♂	..	..	..	24	74	100	100	100	100	100
„ 16 ..	19, juv.	♀	..	..	33	85	100	100	100	100	100	100
J. „ 16 ..	20, ad.	♂	..	..	33	78	100	100	100	100	100	100
„ 29 ..	21, ad.	♂	0	70	100	100	100	100	100	100	100	100
„ 29 ..	22, ad.	♀	..	..	40	82	100	100	100	100	100	100
„ 29 ..	23, juv.	♀	..	..	0	48	87	100	100	100	100	100
M. Feb. 18 ..	24, ad.	♂	..	33	76	100	100	100	100	100	100	100
K. „ 18 ..	25, ad.	♂	67	78	100	100	100	100	100	100	100	100
L. Mar. 4 ..	26, ad.	♂	95	84	100	100	100	100	100	100	100	100
„ 4 ..	27, ad.	♂	67	84	100	100	100	100	100	100	100	100
	Totals ..	..	229	349	617	1022	1601	2212	2414	2503	2639	2651
Number of specimens participating in the moult of respective quills			4	6	11	16	22	25	26	27	27	27
Order of the moults alphabetically expressed			*k*	*i*	*h*	*g*	*f*	(*e*	*d*	*c*)	*b*	*a*

For explanation of Tables on

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of the main quills. O=shed to 100=full growth.

WING.

CUBITALS.

No.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	Totals.
(1)	..	..	..	..	..	..	..	94	93	..	341
(2)	..	..	..	..	..	..	..	78	100	..	542
(3)	..	..	..	..	..	..	..	57	20	..	420
(4)	..	..	..	..	..	..	..	52	20	..	259
(5)	15	..	..	..	..	..	..	100	100	9	718
(6)	34	..	..	..	..	..	..	100	93	..	692
(7)	45	..	..	..	..	..	25	100	100	45	846
(8)	87	..	..	..	..	..	100	100	100	100	1056
(9)	37	..	..	..	..	..	100	100	100	100	882
(10)	68	0	..	..	..	0	75	100	100	0	923
(11)	87	43	..	..	..	..	100	100	100	81	1069
(12)	94	51	13	..	..	..	40	100	100	81	1039
(13)	90	47	..	..	..	..	20	100	100	100	1008
(14)	100	100	38	..	..	..	40	100	100	100	1236
(15)	94	27	..	..	..	..	100	100	100	0	955
(16)	100	94	24	..	..	..	60	100	100	90	1210
(17)	100	100	80	20	..	..	40	100	100	100	1304
(18)	100	70	20	..	..	..	80	100	100	100	1168
(19)	100	100	92	8	..	..	100	100	100	100	1418
(20)	100	100	92	37	..	..	100	100	100	100	1440
(21)	100	100	96	100	..	..	100	100	100	100	1666
(22)	100	90	40	..	..	..	100	100	100	100	1352
(23)	64	51	..	..	..	..	..	100	100	54	1004
(24)	100	100	100	100	78	100	100	100	100	100	1787
(25)	100	100	100	100	100	95	100	100	100	100	1940
(26)	100	100	100	91	13	100	100	100	100	100	1883
(27)	100	100	100	100	?	60	100	100	100	100	1811
	1915	1373	895	556	191	355	1580	2581	2526	1760	29969
	23	18	13	8	3	4	20	27	27	22	Grand Total.
	f	*g*	*h*	*i*	*l*	*k*	*f*'''	*a*	*b*	*f*''	

pp. 356–359, see pp. 354, 555.

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TABLE I. *b*.—Showing the relative lengths of growth

RIGHT

CUBITALS.

Date.	No. & Age.	Sex.	X.	IX.	VIII.	VII.	VI.	V.	IV.	III.	II.	I.
A. Nov. 5 ..	1, ad.	♂	..	93	73	..	..	..	..	..	..	..
„ 5 ..	2, juv.	♂	..	100	84	..	..	..	..	..	..	..
B. „ 14 ..	3, juv.	♀	..	40	68	..	..	..	..	..	..	..
„ 14 ..	4, juv.	♂	..	33	57	..	..	..	..	..	..	..
„ 14 ..	5, juv.	♀	..	100	100	..	..	..	..	..	..	11
„ 19 ..	6, juv.	♂	..	86	100	..	..	..	..	..	..	33
C. „ 19 ..	7, ad.	♂	..	100	100	..	..	.	..	..	..	34
„ 19 ..	8, juv.	♂	100	100	100	100	..	..	..	..	..	98
„ 28 ..	9, ad.	♂	100	100	100	100	..	..	..	..	..	37
D. „ 28 ..	10, ad.	♂	100	100	100	25	..	..	..	..	0	71
E. Dec. 3 ..	11, juv.	♀	81	100	100	100	..	..	..	..	39	83
„ 3 ..	12, juv.	♀	81	100	100	15	..	..	..	..	35	94
„ 11 ..	13, juv.	♀	27	100	100	100	..	..	..	..	35	83
G. „ 11 ..	14, juv.	♀	0	100	100	45	..	..	..	36	100	100
„ 19 ..	15, juv.	♂	100	100	100	90	..	..	..	..	30	90
F. „ 19 ..	16, juv.	♂	36	100	100	50	..	..	..	12	90	94
H. Jan. 1 ..	17, ad.	♂	100	100	100	0	..	..	20	72	100	100
„ 1 ..	18, ad.	♂	100	100	100	40	..	..	..	0	90	100
„ 16 ..	19, juv.	♀	81	100	100	100	..	..	2	92	100	100
J. „ 16 ..	20, ad.	♂	100	100	100	100	..	..	33	92	100	100
„ 29 ..	21, ad.	♂	100	100	100	100	..	..	..	56	100	100
„ 29 ..	22, ad.	♀	100	100	100	100	..	..	..	36	100	100
„ 29 ..	23, juv.	♀	72	100	100	..	..	..	..	..	39	98
M. Feb. 18 ..	24, ad.	♂	100	100	100	100	100	52	100	100	100	100
K. „ 18 ..	25, ad.	♂	100	100	100	100	95	100	100	100	100	100
L. Mar. 4 ..	26, ad.	♂	100	100	100	100	100	13	95	100	100	100
„ 4 ..	27, ad.	♂	100	100	100	100	90	?	100	100	100	100
	Totals ..	..	1678	2552	2582	1465	385	165	450	796	1358	1926
Number of specimens participating in the moult of respective quills			20	27	27	19	4	3	7	12	18	23
Order of the moult alphabetically expressed			*f''*	*b'*	*a'*	*f'''*	*k'*	*l*	*i'*	*h'*	*g'*	*f'*

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of the main quills. O=shed to 100=full growth.

WING.

METACARPO-DIGITALS.

No.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	Totals.
(1)	62	63	O	..	..	..	..	.	..	..	291
(2)	100	100	90	75	35	..	..	..	..	..	584
(3)	100	100	83	59	24	..	..	..	..	..	474
(4)	66	59	40	3	..	..	..	..	..	..	258
(5)	100	100	100	100	71	23	..	..	..	..	705
(6)	100	100	100	97	63	O	..	..	..	..	679
(7)	100	100	100	100	87	38	..	..	..	..	759
(8)	100	100	100	100	100	71	..	..	..	..	1069
(9)	100	100	100	88	54	2	..	..	..	..	881
(10)	100	100	100	100	100	74	2	..	..	..	972
(11)	100	100	100	100	100	58	O	..	..	..	1061
(12)	100	100	100	100	100	56	..	..	..	..	981
(13)	100	100	100	100	100	64	7	..	..	..	1016
(14)	100	100	100	100	100	100	56	2	..	..	1139
(15)	100	100	100	100	87	69	12	..	..	..	1078
(16)	100	100	100	100	100	92	48	..	..	..	1122
(17)	100	100	100	100	100	100	73	33	..	..	1298
(18)	100	100	100	100	100	87	29	..	..	..	1146
(19)	100	100	100	100	100	100	97	60	..	..	1432
(20)	100	100	100	100	100	100	82	35	..	..	1442
(21)	100	100	100	100	100	100	97	76	5	..	1434
(22)	100	100	100	100	100	100	75	35	..	..	1346
(23)	100	100	100	100	100	87	51	O	..	..	1047
(24)	100	100	100	100	100	100	100	81	19	..	1752
(25)	100	100	100	100	100	100	100	100	75	67	1937
(26)	100	100	100	100	100	100	100	86	50	..	1744
(27)	100	100	100	100	100	100	100	100	75	67	1832
	2628	2622	2513	2422	2221	1721	1029	608	224	134	29481
	27	27	27	26	25	23	17	11	5	2	Grand Total.
	a	*b*	(*c*	*d*	*e*)	*f*	*g*	*h*	*i*	*k*	

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Fatio (*l. c.* p. 252) mentions them as "Première livrée de l'enfance," &c. From the same author we also learn that the existence of the down-feathers is very brief, even in those birds whose nestlings retain them during the earlier stages of development, until their actual fledgling-plumage appears.

Structurally, these feathers belong to the filo-plumaceous type (Fatio, pp. 252–254, *l. c.*), giving the young bird the somewhat *silky*[1] appearance of which Fatio speaks.

The filo-plumaceous feathers are either pushed or borne out on the tips of feather-papillæ of the more specialized plumage which follows on. This is formed in the corium. The duration of attachment of the first livery to the new feathers varies considerably; it also varies according to families. (See also Fatio, *l. c.* p. 263.)

In some it is repeated through every feather-change, as in the *Struthionidæ*. In the greater part of the *Carinatæ* this sessile condition is confined to the first change. Cases of three simultaneous attachments of feathers are known to occur occasionally, of which one is mentioned by Wittmer Stone (44), p. 112, for a Meadow-Lark. This author also quotes the case observed by Will. Palmer in the 'Auk,' 1894, of a young Hooded Warbler, *Sylvania mitrata*, in which the *down*[1] of the nestling was to be seen at the tip of the feather of the first plumage, while the latter was "*in turn attached*[1] to the new feather of the winter plumage."

In Struthious birds this latter phase seems to be of frequent occurrence, as I myself have found several instances in the Emu (*cf.* also Fatio, *l. c.* p. 253). These filamentous sessile plumes are to be seen in a young *Columba domestica* figured by Pycraft (39), plate xvi. fig. 1, where they are supported by the main coverts which are sprouting, and reference may also be made to my figure of a young Parrakeet (*Platycercus eximius*) (see text-figures 1 & 2), where they are clearly defined for all the series of coverts and contour-feathers.

I have not myself had the good fortune of proving the existence of these plumes on the rectrices, but an observation was made by Brehm (8), p. 346, on this point in the Owls, whose remark on it in the original is as follows:—

"Die einjährigen Vögel erkennt man übrigens doch *untrüglich* daran dass die *Spitzen ihrer Steuerfedern*, weil der *Nestflaum auf ihnen gesessen hat*, eine *kleine Lücke* in der *Mitte zeigen*"[1].

The important nature of this passage resulted in a footnote from the Editor (Dr. Cabanis) to the following effect:—"Eine etwas *suptile Wahrnehmung*," &c.; and further, "die ober wohl beachtens werth scheint und jedenfalls wiederum von der anerkannt *scharfen Beobachtungsweise des Verfassers zeugt*"[1].

Yet the *nicety* of this observation of Brehm, as pointed out by Dr. Cabanis, gains in strength materially if we turn to a statement made by Blyth (4), who, on p. 260, in

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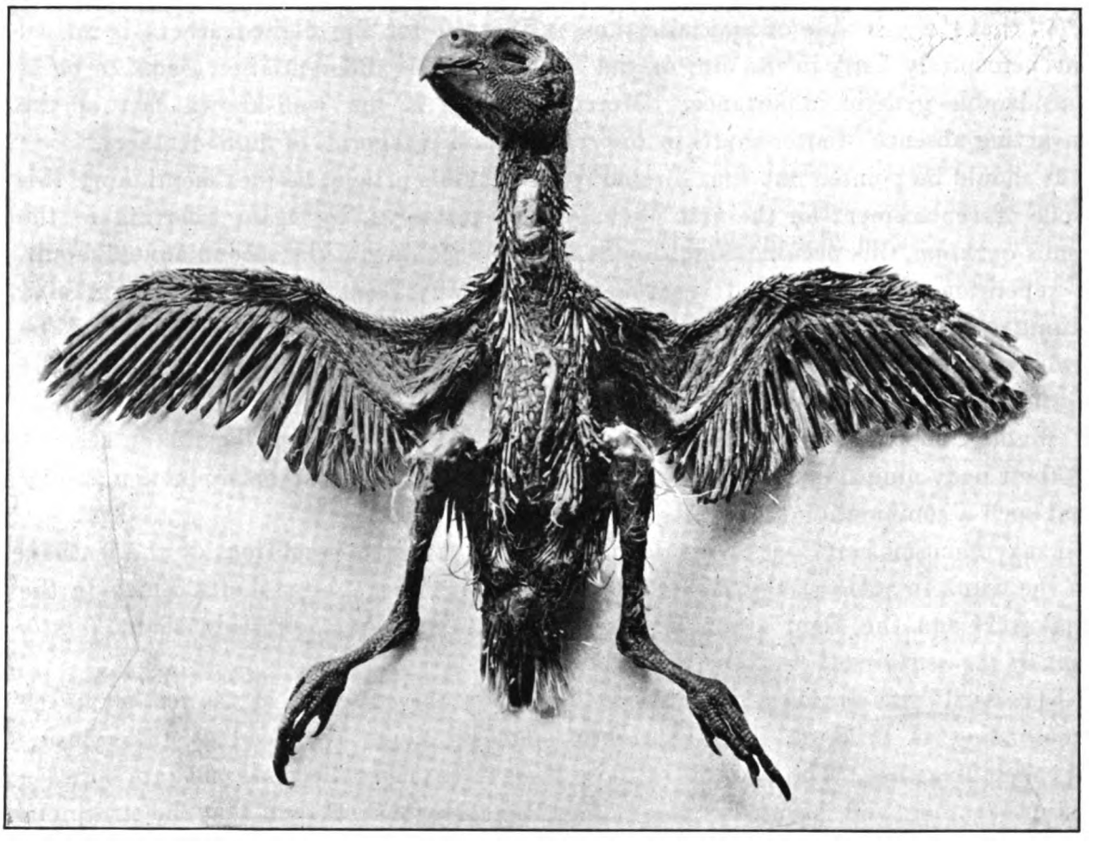
referring to the feather-changes in general, says :—" In the Widgeon, however, and many other species, it will be found that the adult livery is obtained, in spring, by an actual change of plumage, every feather being cast and renewed, except, of course, the *wing* and *tail-primaries* [1]. And here it may be remarked that the *two central caudal feathers* [1], which in all birds visibly differ from the rest, being of softer texture

Text-fig. 1.



Young Parrakeet, showing the filamentous plumes (neossoptiles) carried on the tips of the new contour-feathers.

and commonly of another colour, *partake of the nature of the tectrices and wing-coverts* [1], and in double-moulting species are, like them, very usually shed and renewed with the vernal renovation of clothing-plumage," &c., &c.

Now, whether or not, Brehm, in his observation of *Syrnium*, using the general term of " rectrices " (Steuerfedern), had in mind the two centrally situated caudals only, does not appear; in any case, it would seem that so far Blyth's observation of the value of these was fully confirmed.

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If it could be shown that the "primary" value of feathers could be established by Brehm's observation, we should become possessed of a good test for their serial value. Having paid attention to this feature whenever a favourable opportunity presented itself, in no case have I met with the sessile condition of these early plumes on the flight-feathers, though they are present invariably on the main coverts, both dorsal and ventral, according to my observation.

If, so far, we are supplied with even this slight means of differentiation between the remiges and the rest of the covert- and contour-feathers, then we should have ample proof that the principle of specialization, at any rate for the flight-feathers, is carried out perceptibly early in the life of the bird; and this differentiation seems to be of considerable genetic importance. Moreover, there is the well-known fact of the unvarying absence of after-shafts in the case of both categories of flight-feathers.

It should be pointed out that Brehm (7 & 8) in his article, besides mentioning this mode of replacement for the first plumage, also instances, by again referring to the genus *Syrnium*, this peculiar condition as taking place during the second annual moult. A repetition of this kind of renewal then naturally leads to the assumption of a primitive condition of the plumage, to which the soft and downy feathering of the Owls certainly points. And if we were to apply the existing analogy to some of the *Ratitæ*, the theory as to their descent from a bird which once possessed the power of flight (Gadow (21), p. 667, quoting Fürbringer) is not the less tenable on account of their body-plumage still retaining this primitive style of feather-production, seeing that such a combination still exists for the Owls.

I may mention here that owing to the yet more primitive conditions of the feathers on the trunk in some of the *Ratitæ*, the extreme tips of the after-shafts, which in the Cassowary and the Emu attain a length equal to that of their main shafts, *jointly support the new-growth feather* [1] with the latter.

Necessarily this throws a curious side-light upon the structure of the feather in the Struthiones, as Beddard (3), p. 18, rightly suggests, under the heading "Pterylosis," by concluding that "The feathers of those birds have been called intermediate between contour-feathers and downs. *It may be that they are primitive* [1], and that the struthious birds have arisen from some ancient type *in which the modern bird's feather had hardly been evolved*" [1].

To a great extent, then, will this help to solve the true relationship of the after-shaft to the main shaft (*cf.* also Nitzsch (37), pp. 8 & 9). The importance attaching to the bifurcated follicle, as shown in the beautifully executed drawing of its desiccated cells, known as the "soul" in the quill by Holland (29), on table i., figs. 2 *b* & 3 *b*, becomes at once fully apparent. Their union occurs in the *cavum calami* within the "*corpus calamus*," of which the one branch deposits the *substantia rhachidis externa* for the

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main, and the other the same substance required in the building-up of the after-shaft. In speaking of the latter, Holland, on p. 346, *l. c.*, says: "Bei Federn mit Afterschaft bildet sich dem ersten gabelförmigen Streifen gegenüber am Bauche des *folliculus* noch ein zweiter ähnlicher Längsstreifen, an denen dieselbe Bildung vorgeht, wie wir eben gezeigt, und der *folliculus* lagert nach seiner vorderen und hinteren Seite Mark ab. *Wo das corpus calami beginnt verwachsen beide Schäfte zu Spule*" [1].

Any doubts existing as to the structural plan of the primitive contour-feathers are dispelled consequently by the retention in the Cassowary and the Emu of the original feather-structure. *This was a duplicated organ* (see also Nitzsch, p. 9), *of which the two component parts*—in the birds alluded to—*are still of equal length and strength* [1]. These latter qualities are carried out to such a point of perfection that it is really difficult to determine which is the *rhachis* and which the *hyporhachis* [2].

For the reduction of the latter (to $\frac{2}{3}$ the length of the main shaft in the Grouse), to its total disappearance, we get every degree of perfection in the development for the main shaft of the feather towards that highest of degrees, as attained by the *Oscines* amongst the Passerine birds at the expense, as it were, of the after-shaft. This more highly specialized and simple form of feather, as acquired in recent types of birds for perfected adaptation to flight, is then really only one-half of the feather, and, however incongruous the inference may be, is a degeneration from the original duplex structure.

B. *On the "Feathering of the Fledgling."*

A probably common feature of all the Carinatæ is the mode in which they acquire the first set of flight-feathers. The supply of this first set of quills on the wing is generally concurrent with the appearance of the greater portion of the contour-feathers in the principal tracts of the trunk and on the head.

In the *Gymnopædes* the remiges appear somewhat in advance of the latter. They also appear simultaneously with the upper major coverts by practically the whole series shooting out along the posterior margin of the fore limb and in synchronism (see text-figure 2, p. 364, of young Parrakeet). Indeed, the upper major coverts even precede the remiges in some birds, judging from a statement made and figures given by Pycraft (39) (*cf.* footnote, p. 251, & pl. xvi. fig. 1, *l. c.*) in the case of the young of the Common Fowl and that of a Pigeon. This I can also confirm from my own

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[2] In feathers of equal lengths for the two parts, such as in the Emu, it can be reliably ascertained only when *in situ*. As a symmetrical structure consisting of two equivalent parts, it naturally follows that their ventral or, more correctly designated, *inner sides* face each other, whilst the outer sides (dorsal for the main, ventral for the accessory feather) are averted, irrespective of the convexity of their surfaces, which is a concentric one for both.

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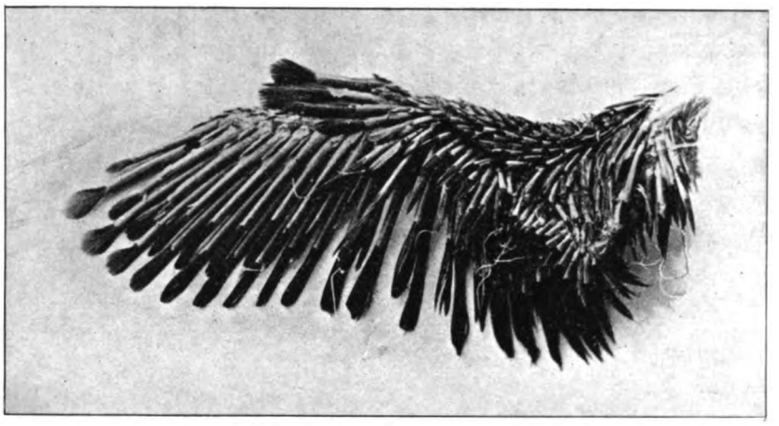
observation. This mode of a first acquisition of flight-feathers equally applies to the rectrices.

The birds known as *Nidifugæ*, like the *Gallinæ* and most of the game-birds, acquire their flight-feathers shortly after emerging from the egg. The young of the Argus Pheasant is an instance in which flight-feathers make their appearance immediately upon leaving the egg. But we have evidence of much earlier development of flight-feathers than that mentioned above. This is seen in the *Megapodes* (and very probably too amongst the *Cracidæ*), whose young acquire their first set of remiges *before*[1] they leave the egg. To this character the term of "*Ovifugæ*" might reasonably be given. Whether or not this first plumo-pennaceous garb be præ- or post-incubate, matters little; it invariably is heralded in the *Dasypœdes* by the adventitious plumage referred to above as the truly embryonic one.

Text-fig. 2.



Dorsal view of the left-side wing of a young Parrakeet, showing the sessile filamentous plumes of an adventitious plumage (neossoptiles) on the tips of the upper covert-feathers.

The function of the first set of flight-feathers with their principal coverts in the fledgling being practically the same as that in the more matured individual, structurally it is, nevertheless, inferior and more primitive in texture than that acquired by subsequent moults. The vanes of the feathers are generally broader, their tips more rounded, the barbs and barbules present a looser union than those which eventually replace them (see remarks made on this point by Brehm (7, 8), also Fatio (19), p. 254). The body-feathers are similarly inferior in substance. Wittmer Stone (44), on pp. 115–117, makes the following statement:—"The remiges and rectrices of the first plumage are usually the same as those of the adult, *but the body-feathers*, while of the ordinary structure, *are much more plumulaceous*[1] than the covering of the adult"—deficient

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not only in warmth of colour, but also in that lustre which imparts to them a finish which makes them distinguishable even to the "touch alone" from the adult birds (Altum (2), p. xxi). In a word, it is a provisional plumage.

Its duration, according to the quotations of the different writers, seems to vary for the families, the genera, and also for the different species amongst the latter; but on this head, owing to observations being frequently based on unreliable material, there is great confusion.

According to Brehm (8) this first or fledgling-plumage is replaced in the genus *Strix* by another of similar primitive quality—an observation which again called for a foot-note from Dr. Cabanis (p. 344, *l. c.*), in which he gives expression of genuine surprise in the following manner:—"*Also zwei Dunenkleider!*"[1] &c., &c. "*Das ist in der That sehr bemerkenswerth*," &c. But Brehm also showed that in the young of the *Owls* the flight- and the tail-feathers, as well as the body-feathers, are shed in the same season in which the bird was hatched, while in the *Birds of Prey* only the body-feathers, excluding the remiges (and probably, too, the tectrices), are shed, these latter being shed in their second autumn (Brehm (7), p. 196, & (8), p. 345). This statement of Brehm was published only a year after the one in which Schlegel (40) made the sweeping assertion that "*the young birds moult for the first time in the autumn of that year which follows the one in which they were born*"[1]. As the aforesaid statement formed one of the fundamental tenets of Schlegel's theory for the alleged regeneration and revitalization of the bird's feathers, it should scarcely be surprising to find that no sooner had it been published than it drew a host of contradictions, not only from Brehm, but also from the ablest observers amongst ornithologists of the time. Amongst the latter was Homeyer (30 *a*), who, after enumerating a considerable portion of the birds composing the list of genera and species claimed by Schlegel for changing colour *without* moult, irrevocably proved this colour-change *with* moult by emphasizing on p. 117 of the article, under the heading of "allgemeine Grundzüge," &c., on the first feather-change in the following conclusive words:—"6. Alle kleineren und viele grössere junge Vögel *mausern vollständig im ersten Herbste ihres Lebens*."

My own observation also disproves Schlegel's statement in regard to this wholesale assertion. To the list, therefore, of birds which undergo their first total moult in the season in which they are reared, I can add also *Gymnorhina tibicen*, the species which has been under my particular consideration and upon which I base this paper.

C. *On "Perennial Feathering."*

The manner in which the feathers on the wing of a fledgling bird are replaced in subsequent changes is strikingly different from that in which they acquired them at

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first. It differs from it in shedding and eventually substituting the quills one by one, sometimes two, even three or four at a time, occasionally but rarely more. Some exceptions to this rule occur amongst the *Chenomorphæ* (Schlegel (40), p. 20, *l. c.*, also mentions the *Anatinæ* as exceptions), where the juvenile condition of shedding the flight-feathers in greater numbers seems to occasionally recur with the periodical moult. A case of such a seemingly abnormal character has been observed by Wiese, on an old Crane ("Beiträge zur Ornithologie Pommern's," J. f. O. 1855, iv. Heft, No. 18, p. 515). But, as has been pointed out by Gloger (26), p. 392, when remarking on this case: "These birds have other means of locomotion than flight alone." Quite recently I had an opportunity of seeing a like condition in a Moorhen, kindly brought to my notice by Mr. C. H. Grant in the Natural History Museum, who regarded the occurrence as an exceptional one. The fishermen of the lake-entrances and inlets on the south coast of Australia know this fact so well that in the case of the Black Swans (*Chenopis atrata*), which are so numerous there, they frequently take advantage of the temporary impediment to which the "Moulter," as the bird is called at this time, is subjected, and amuse themselves by running it down in their sailing-craft—a very exciting sport.

With regard to perennial moult, Schlegel (40) says, p. 20: "6. The order in which the flight-feathers are shed and replaced is that of bilateral symmetry." Beyond this general statement he has nothing further to say with regard to this important factor in the feather-change. The observation that the flight-feathers were replaced in an irregular sequence of their order, belongs to Gerbe (23). Although his observations extended to a general comparison only between the *Gallinæ* and *Passeres*, it is noteworthy, nevertheless, to find how greatly he was struck by the peculiarity of order in which the moult proceeds on the forearm. This order he describes thus: "7°. A l'avant-bras, la mue chez les Passereaux ne commence généralement que lorsque la cinquième des primaires vient de tomber. *Elle se manifest à la fois sur les deux points extrêmes du cubitus et prend deux directions qui tendent l'une vers l'autre*[1]: d'un côté elle se poursuit de la première de *secondaires* (*cubitals*)[1] à la sixième inclusivement; de l'autre de la neuvième ou dernière à la septième."

For a considerable extension of our knowledge on this point we are indebted to the researches made by Wittmer Stone (44), who regards the laws and principles which govern ecdysis as, what he rightly terms for the bird, "*a physiological necessity, common to all*"[1]. But in attempting to deal with it in general as he has done, the ground cannot be considered as sufficiently prepared until all the phases are known through which the individual passes.

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VI.—"Orders of the Moult" in *Gymnorhina tibicen*.

A. *Flight-feathers or Pennæ alares = Remiges primores plus Remiges cubitales* (Sundevall).

The relative lengths of the flight-feathers on the manus are in the order below from left (the longest) to right (the shortest), thus:—

7—6—8—5—9—4—3—2—1—10.

The manner in which the remiges make their appearance is regulated by a definite order in both portions of the wing. As might have been expected, the bilateral symmetry assigned for the individual (*cf.* Schlegel, 40, p. 21) is not strictly observed. But there is at no time any considerable departure from the broad principle. Besides this general bilateral form of symmetry, there is one existing also for the two portions of each wing *inter se*, viz. the hand and the forearm. It is present during the earliest stage of the moult in the case of primaries I. and II. and secondaries VIII. and IX., the remiges corresponding with each other for moulting first, as represented by specimen No. 1.

Diagr. A (stage *a* and *b*). (Lettered on Plate XXXVI. *a*, *b* and *a'*, *b'* respectively.)

The fully adult specimen No. 1 (left and right wing) showed this earliest stage remarkably well; younger ones not complying with the rule so exactly, as No. 2 proves, and also the following one, shot on the same date, mostly young birds.

Diagr. B (stage *c*, *d*, *e*). (Plate XXXVI.)

The parti-lateral symmetry of the first stage becomes soon disturbed by the appearance, in rapid succession, of primaries III., IV., and V., lettered in the Table *c*, *d*, and *e* respectively, *these having no equivalent renewal on the cubitus*[1]. Four specimens show this arrangement remarkably well, of which No. 4, a very young male, does so in part only. The diagram represents specimen No. 3.

Diagr. C (stage *f*). (Plate XXXVI.)

The next stage, that of *f*, which comprises the replacement of primary VI., is a particularly interesting one, insomuch as it marks the restoration of the parti-lateral symmetry by an almost simultaneous development of three secondary remiges. These are cubital remiges I. or *f'*, X. or *f''*, and VII. or *f'''*. *Their synchronous appearance therefore is a compensation for primaries*[1] III., IV., and V. It is marked best in the left wing of specimen No. 7, Plate XXXVI., as shown in the diagram C, which represents this third stage or that of *f* and its equivalents. This also explains the reason why these remiges are equivaluated *f'*, *f''*, and *f'''* respectively (the dashes representing

[1] The *italics* are mine.

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their sequence of growth), and not, as one would have expected *c'*, *d'*, and *e'*, were they making their appearance in synchronism with *c*, *d*, and *e*. Four specimens show this phase of moult, viz. Nos. 7 (diagr. C, Plate XXXVI.), 8, 9 (partially in arrear), and 10 (see also Plate XXXVI., diagr. D), partially in advance of development. So well, however, does the latter one (No. 10) mark this stage and also the following, viz. that of *g* in its beginning, which latter is the moult of primary VII., that it has been added also to the series of diagrams, in which it is marked D, as illustrating a case of transition for the two stages.

DIAGR. D, showing transition between stages *f* and *g*. (Plate XXXVI.)

This represents specimen No. 10, and referred to above. This individual is very asymmetric in moult, both for bilateralism and left-sided development. It exhibits the somewhat rare occurrence on its left-side cubitus of synchronously shedding no less than three remiges: viz. X. belonging to stage *f'*, II. stage *g'*, and very prematuredly VI., as belonging to a much later stage, *i. e.* that of *k'*. Its right side fairly agrees with the normal condition.

DIAGR. E (stage *g*). (Plate XXXVII.)

Stage *g*, or the replacement of metacarpo-digital remex VII. and synchronous in growth with cubital remex II. (*g'*) (as referred to for the last specimen, No. 10), is not clearly defined in either of the five or six individuals which share this phase of the moult. For instance, in No. 12 this phase is shown in the cubital portion only; while in its hand portion the changes are in progress only as far as remiges VI. on both sides. Similarly No. 13 for its left side, while the right side of this specimen shows stage *g* in a normal condition.

An otherwise clear case of this stage of development obtains for specimen No. 15; but this individual, being a later acquisition than No. 14, which represents a typical case of the next following phase, or that of *h*, I have consequently not admitted to the diagrams, because of the desirability for conforming to the order in the succession of the dates as near as possible.

Specimen No. 11 therefore has been substituted to supply the present *Diagr. E*, Plate XXXVII., as supplementing the part development of this stage of *g*, referred to in the previous diagram D.

DIAGR. G (stage *h*). (Plate XXXVII.)

The next phase in the moult is that of metacarpo-digital remex VIII., or stage of *h*, which appears in regular sequence in the numerical order of the feathering of the hand portion. Corresponding in synchronous development on the cubitus with this quill is remex III., lettered *h'*.

As mentioned above, specimen No. 14 shows this phase distinctly, though in its

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early growth. This is particularly the case for the primaries, on both sides, which are just issuing; whilst cubital remiges III. have already attained about $\frac{1}{3}$ of their ultimate lengths. Being, however, developed quite symmetrically, the specimen was better adapted for a concise diagrammatic representation of this stage than other and later ones, which blend more or less with either the earlier stage of *g* or the later one of *i*.

DIAGR. F (supplementing stages *g* and *h*). (Plate XXXVII.)

The specimen which supplies this diagram is No. 16. It is one showing the phases of transition between *g* and *h*. This specimen repeats and completes the stage of *g*, while that of *h* is developed in part. It therefore precedes for stage of development of specimen No. 14, diagr. G, on the same Plate, although forming part of a complement of specimens which were received at a later date.

DIAGR. H (illustrating stage *i* partially). (Plate XXXVII.)

In specimen No. 17, which this diagram represents, we have an individual which should mark the next phase in the moult of the primaries, namely that of metacarpo-digital remex IX. or *i* if under normal conditions. But this individual being in arrear of moult for the hand portions (metacarpo-digital remiges IX. being as yet undeveloped) it merely shows this phase of renewal for their corresponding remiges IV. or *i'* on the cubitus. It has been diagrammatized, nevertheless, for helping to complete the illustration of this stage of development, which is one not very clearly accentuated in either of the specimens which partake of it. For instance, Nos. 18 and 19 are considerably in arrear of moult; the latter, however, is distinguished by showing stage *i* partially on the cubitus. No. 20 agrees with No. 19.

DIAGR. J (supplementing stage *i*). (Plate XXXVIII.)

In specimen No. 21, which this diagram represents, we have a case in which the conditions for stage *i* are reversed: since remex IX. is in full process of growth in the hand portion of the left wing; whilst it has just issued on the right wing, the side in which it is usually more in arrear than the other. The moult for cubital remex IV. or *i'*, the corresponding one for that of the hand portion, has not yet set in for the right side. This specimen, then, together with that shown in *Diagr. H* (the former one), supplement each other in the completion of stage *i* and *i'* respectively.

No. 22, in arrear of moult, conforms to stage *h*, but is conspicuous as showing a case of almost perfect bilateral symmetry.

No. 23 is further in arrear, having reached stage *g* only.

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DIAGR. K (stage of *k*). (Plate XXXVIII.)

In specimen No. 25 the successive growth of metacarpo-digital remex X. or stage *k*, and the last to be replaced for this series, we possess a particularly well-defined case of absolute bilateralism of symmetry. The development of this flight-feather has reached exactly the same length on both sides. Its synchronous equivalent on the cubitus, namely remex VI. or *k'*, has also been developed in perfect symmetry, having nearly obtained its full growth. The metacarpo-digital remiges IX., also symmetrically developed on both corresponding portions of the wings, are yet incomplete, though porportionately further advanced than X., and beautifully show the regular order of their successive growth. This particularly typical specimen deserves special attention.

A glance at the diagram of this last specimen will at once disclose the fact that the replacement of the flight-feathers, which at this stage is merely completed for the hand portions, is incomplete for the cubitus, where a gap is left still for the filling in of remex V., which is the last one to appear in this section of the wing. The earlier accomplishment of the moult of the flight-feathers belongs, therefore, to the hand portion, both in its initiating as well as its concluding stages. This is the case with three specimens out of four which participate in this last phase. These are Nos. 24, 25, and 26 (left wing), and which have all been diagrammatized chiefly for showing the growth of cubital remex V. in its earliest relationship to the others; and lastly, No. 27, which also shows a further case of perfect bilateral symmetry. It has been found necessary to give a diagram of No. 24, because it shows the final stage in filling up the gap by cubital remex V. Again, this stage, having practically no synchronous equivalent on the hand portion as above mentioned, required the application of the additional letter *l'* to mark this supernumerary condition.

DIAGR. L (stage of *l'*). (Plate XXXVIII.)

This represents specimen No. 26, and shows this stage in its beginning, the secondary remex V. being of equal development on both wings.

The growth of primary X. is nearly complete for the left wing; whilst its development on the right side is considerably retarded.

DIAGR. M (supplementing stage of *l'*). (Plate XXXVIII.)

As indicated above, specimen No. 24, though imperfect for the completion of the moult on its hand portion, but otherwise very symmetrically developed, forms a case for further progress in the final stage of *l'* or cubital remex V. It is curious to note how early this specimen has reached this stage, being of February 18th, when compared with 26th and 27th, which were both received a week later, namely March 4th.

As already stated, the specimens completing the List of Birds examined, which were received as late as the end of April, had their moult positively completed,

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EXPLANATION OF TABLE II.

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1. The *vertical lines* form the divisions for the whole period of the moult for the remiges, consisting of 28 weeks.
2. The *horizontal bars*, situated between any multiple of vertical lines, represent the respective remiges, whose ordinal number, in Roman figures, is placed in the lefthand-side column, as counted from the wrist-joint.
3. The letters to the right side of the table denote the order in which they moult, by plain letters, and alphabetically arranged for the metacarpo-digital—with one or more dashes (thus, ′, ″, ‴) for the cubital portion of the wing, and also in their synchronizing order of moult with that of the hand-portion.

   The *darts* on the right side of these letters are indicative of the direction of their moult for the groups of which these remiges form an integral part. (See also Plates.)
4. *Top line*: names of months for the period during which the perennial moult of the flight-feathers proceeds in *Gymnorhina tibicen*.
5. The *numbers* entered on the *second line* are the dates of those months on which the specimens were received and examined.
6. The cyphers on the *third line*, in addition to the number of weeks which each particular quill requires for its development (collective time for the species) from its first appearance to its full growth, also serve for comparing chronologically any two or more quills between the metacarpo-digital and the cubital portion of the wing, or *inter se*.

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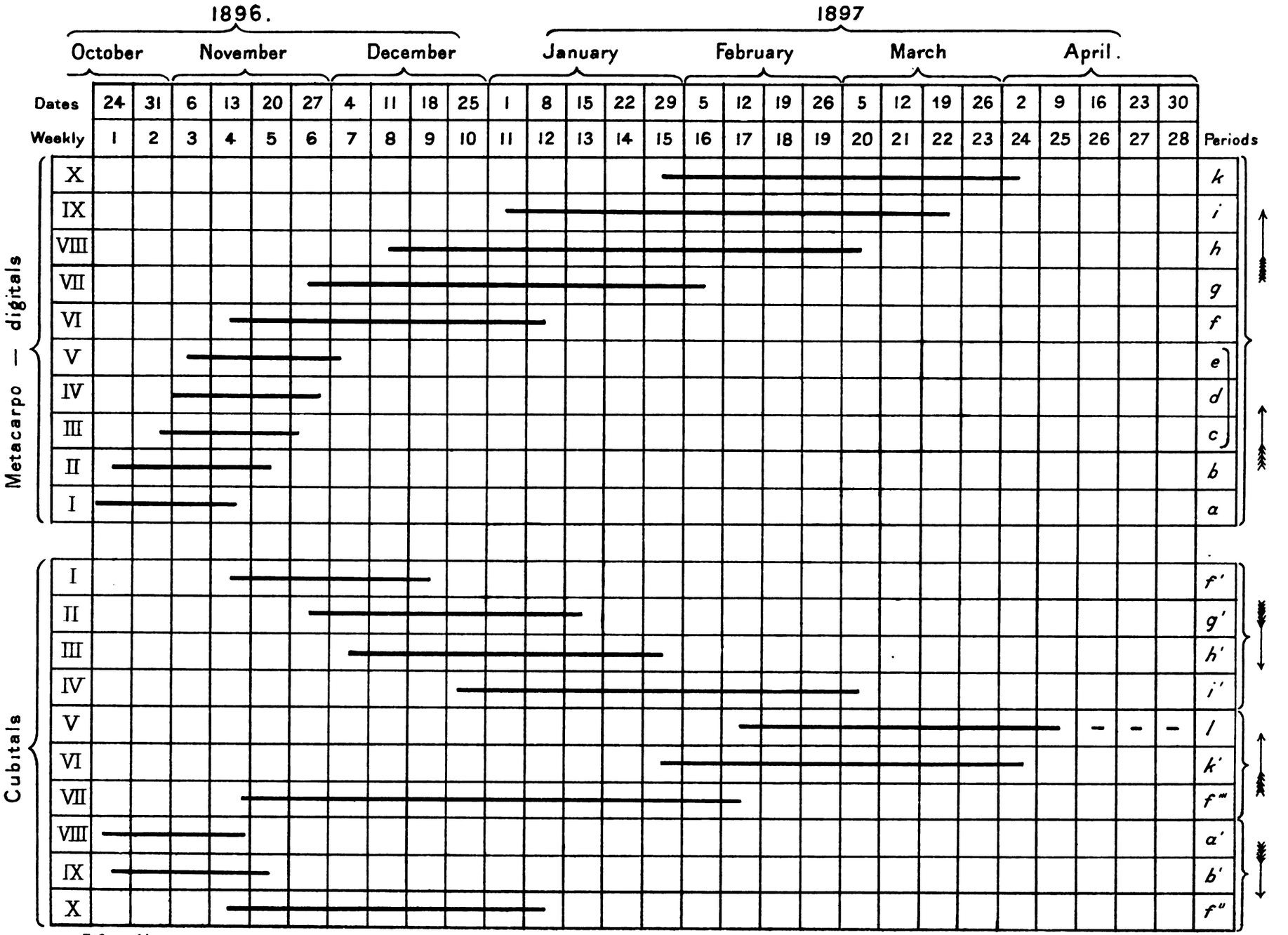
TABLE II.

To face p. 370.



Chart, setting out the Period of Growth, and Chronology in the Development of the Main Quills.

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though in the case of Nos. 28 and 29 the cubital remiges IV. and V. were still somewhat short of their ultimate lengths.

B. *Remarks on the Period of Growth and the Development of the Remiges.*

Although the actual time required for the production of each quill itself cannot be followed with precision in the dead animal, neither is such the case with a bird in captivity, owing to altered conditions. But this can, nevertheless, be estimated tolerably well from a number of specimens which show a particular quill to be in moult within a given stage; and, further, with the aid of a quill just recently developed to full growth, as is the case in the majority of individuals showing more than one quill in successive stages of development at the time, and another one perhaps just emerging, when we get a valuable means for obtaining, by differential inference, an approximate result for the individual.

From the averages extracted for the period of growth for each quill, the result shows that those of the earlier stages develop faster than those of the later ones, which take somewhat longer to grow. The difference, however, is not considerable, and fluctuates between seven and ten days respectively. The range of time for the moult of the different remiges during a seasonal change can also be computed for the species as a whole, and a chart (Table II.), setting out the general result, having the additional advantage of showing their synchronic movements, has been appended also at the end of these remarks.

C. *The "Bastard Wing."* Alula *or* Ala spuria = Plumæ pollices.

In all robustly and normally developed individuals of this species I have never failed in finding the regular number of *pennæ*, which constitute this series, to be less than four. It is in weakly developed individuals only that their number is occasionally reduced to three. In such cases it is invariably at the expense of the innermost, or the first one if one regards them in the same light as the metacarpo-digital remiges.

Had there any additional proof been wanting on the remigial nature of these feathers, apart from a previous observation of the most proximal ones being sandwiched in between an abortive upper and a homologous ventral covert, nothing could have been more fortunate for dispelling the doubt as to their true value as flight-feathers than that shown by their moult.

When I had received specimens representing the progressive stages of the moult for a consecutive number of weeks without having met as yet with any evidence on this point, I began to entertain serious misgivings of having missed what I then considered to be one of the most desirable points in this investigation.

As these feathers, it seems but reasonable to assume, are not greatly exposed to wear, it is at all times difficult, as I found, to distinguish between their old and their new growths, unless one secures the bird during their actual renewal.

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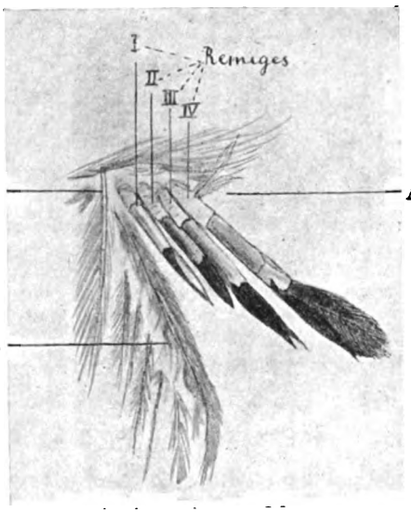
It was a great satisfaction to me therefore when, on December 11th, I received the first specimen of a young female, numbered 14, which showed evidence of the moult for three out of the four feathers on both wings. A second bird, forming part of the same weekly complement, and which had received the serial number 13 on account of having been examined before the former, also a young female, exhibited no traces of moult for this part. This difference may be accounted for by the latter specimen being more backward in moult than No. 14 as regards one or two of the metacarpo-digital and one of the cubital remiges.

The next weekly instalment, consisting of four specimens, contributed nothing further to this stage of the moult. Curiously enough, another young female, No. 19 of the series, supplied the desired evidence for the whole of this set of feathers in such an excellent manner for both wings alike that nothing could be more perfect for a demonstration of the graduated succession of their growth, as seen in text-fig. 3, from my drawing of its right wing.

Text-fig. 3.



Showing the successive stages of development of the quills composing the Alula, from without inwards.

The figure shows the fourth longest and outermost feather, if not perfectly freed at its base from the *capsula*, to have at least acquired its ultimate full length. The next inner one, whose adhering capsule remains and encloses a greater amount of the new growth in proportion to the former, shows it to be about $\frac{3}{4}$ of its eventual length. The third innermost, being remex II., and the next in rotation of development, has attained one-half of its length; whilst remex I., or the innermost and last to appear,

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has only reached the stage of development of a pin-feather, whose extreme barbs have just pierced the tip of its accompanying capsule. In text-fig. 3 these feathers are marked respectively, remiges IV., III., II., and I., in the order described above.

Another specimen received on the same date (January 16th) as the previous one, to which I have given the serial number 20, also shows the whole of this set in full process of moult on both sides of the wing, but is in a rather more advanced stage throughout.

Two specimens, Nos. 21 and 22, dating from January 29th, out of the total complement for that week, which also includes No. 23, also partake in this phase of the moult. No. 22 is slightly belated if compared with No. 20, whose early-accomplished *pennæ pollices* correspond with the moult of metacarpo-digital remiges V., VI., VII., and VIII. respectively; whilst in the case for the left side of No. 21, they correspond with primaries VI., VII., VIII., and IX. The right side is later still, where the 4th feather is the only one as yet replaced; this corresponds with metacarpo-digital remex VII.

Specimen 22, for an old female, presents a case of later appearance still, and, moreover, shows the additional anomaly of simultaneously producing (but symmetrically for both sides) the fourth and the second quills, whereby it has missed the renewal of the intervening third quill. The impending moult of this latter is indicated by its point just showing above the epidermis on the right side only, thus, as it were, rapidly remedying the deficiency. Seeing that this is the only specimen out of four quite normally moulting individuals, this case can be little else than the result of a faulty individual constitution.

In the remainder of the specimens received after this period, the moult of this series of feathers was invariably accomplished. It, moreover, shows that their moult is identical in period with that of certain primary remiges, and corresponds almost exactly with the extreme digital ones by slightly fluctuating between metacarpo-digitals VI. and X.

The relative position for the growth of these pennæ pollices to those primaries with which they moult in synchronism, based upon the highest aggregates received for each feather separately, will be found entered on Table VI., which is at the end of the technical description dealing with the feather-tracts in general.

The moult of these *pennæ* is of ever so much greater importance than their purely ordinal replacement when considered from the point of digital feathering as a whole. Whether the origin be a doubtfully remigial [1] or an admittedly tectrical one only is of no consequence in this place. At the most their metacarpo-digital value must remain undisputed, since the principal satellites, as will be seen, also reflect the ordinal

[1] The similar absence of sedentary neossoptiles on the tips of the first set of these feathers, the same as in the other remiges, ought, in my opinion, to be decisive on this point.

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TABLE III.—Showing in Percentages the Deficiency in the Power of Flight during the various Stages, caused through the Perennial Moult of *Gymnorhyna tibicen*.

Date.	No. of specimen.	Sexes and Ages.	Left Wing.			Right Wing.			Grand Totals for both Wings.
			Metacarpo-digitals.	Cubitals.	Totals.	Cubitals.	Metacarpo-digitals.	Totals.	
1896. Nov. 5 ..	1	♂ ad.	14·6	1·3	7·9	3·4	17·5	10·4	9·1
„ „ 5 ..	2	♂ juv.	13·6	2·2	7·9	1·6	10·0	5·8	6·8
„ „ 14 ..	3	♀ juv.	15·7	12·3	14·0	9·2	13·4	11·3	12·6
„ „ 14 ..	4	♂ juv.	21·3	12·8	17·0	11·0	23·2	17·1	17·0
„ „ 14 ..	5	♀ juv.	10·6	17·6	14·1	8·9	10·8	9·8	11·9
„ „ 19 ..	6	♂ juv.	13·5	7·3	10·9	8·1	14·0	11·0	10·9
„ „ 19 ..	7	♂ ad.	6·9	18·5	12·7	6·6	7·5	7·0	9·8
„ „ 19 ..	8	♂ juv.	3·1	1·3	2·2	·2	2·9	9·5	1·8
„ „ 28 ..	9	♂ ad.	5·5	6·3	5·9	6·3	15·6	10·8	8·3
„ „ 28 .	10	♂ ad.	12·0	35·7	23·8	20·4	12·4	16·4	20·1
„ Dec. 3 ..	11	♀ juv.	14·2	8·9	11·6	9·7	14·2	12·9	12·2
„ „ 3	12	♀ juv.	4·0	22·9	13·0	17·5	4·4	10·9	11·9
„ „ 11 ..	13	♀ juv.	4·9	14·3	9·6	15·5	12·9	14·2	11·9
„ „ 11 ..	14	♀ juv.	24·2	13·0	18·6	21·9	14·2	18·0	18·3
„ „ 19 ..	15	♂ juv.	16·6	17·7	17·1	9·0	13·2	11·1	14·1
„ „ 19 ..	16	♂ juv.	5·8	14·2	10·0	20·8	6·0	13·4	11·7
1897. Jan. 1 ..	17	♂ ad.	13·6	16·0	14·8	20·8	9·4	15·1	14·9
„ „ 1 ..	18	♂ ad.	10·2	13·0	11·5	17·0	8·4	12·7	12·1
„ „ 16 ..	19	♀ juv.	8·2	10·0	9·1	12·5	4·3	8·4	8·7
„ „ 16 ..	20	♂ ad.	8·9	7·1	8·0	7·3	8·3	7·8	7·4
„ „ 29 ..	21	♂ ad.	13·0	·4	6·7	4·4	12·2	8·3	7·5
„ „ 29 ..	22	♀ ad.	7·8	7·0	7·4	6·4	9·0	7·7	7·5
„ „ 29 .	23	♀ juv.	16·5	13·1	14·8	9·1	16·2	12·6	13·7
„ Feb. 18 ..	24	♂ ad.	9·1	2·2	5·6	4·8	10·0	7·4	6·5
„ „ 18 ..	25	♂ ad.	5·5	·5	3·0	·5	5·8	3·1	3·0 (5)
„ Mar. 4 ..	26	♂ ad.	2·1	9·6	5·8	9·2	6·4	7·8	6·8
„ „ 4 ..	27	♂ ad.	4·9	4·0	4·4	1·0	5·8	3·4	3·9

For explanation of Table III. see p. 375.

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sequence for renewal, as do the flight-feathers themselves, with the same constant accuracy of recurrence in the species. *As such, then, we have the astonishing fact standing, that they moult* (as may be seen from the drawing) *in an opposite direction to the metacarpo-digital remiges.* This is in no way an isolated occurrence, but a condition which one finds twice repeated on the cubitus, and which, as I believe I am justified in regarding, affords us the *key to the original*, if not *pentadactyle*, at least *tetradactyle feathering* of some ancestral type of birds.

D. *Extract from and Remarks on the Table of Percentages for the Deficiency in the Power of Flight.*

When consulting the foregoing Table (III.), it will be noticed that for both the lowest and the highest percentages the figures are distributed fairly equally without having any direct bearing upon either stage of moult, age, or sex of the individual. Thus we get minima and maxima at all times during the changes.

The *lowest* figures we get are as follows:—

	Metacarpo-digitals.	Cubitals.
Left side	2·1 (26)	·4 (21)
Right side	2·9 (8)	·2 (8)

Totals for left side.	Totals for right side.	Grand total.
2·2 (8)	3·1 (25)	3·0 (25)

The *highest* figures thus received are:—

	Metacarpo-digitals.	Cubitals.
Left side	24·2 (14)	22·9 (12)
Right side	23·2 (4)	20·8 (16 & 17)

Totals for left side.	Totals for right side.	Grand total.
23·8 (10)	17·1 (4)	20·1 (10)

(The figures within the brackets indicate the number of the specimen.)

It will be seen that, while the greatest amount of feather-loss incurred at any time during the moult occurs on the hand-portion of specimen No. 14 with 24·2 per cent., the cubital portion is only slightly behind this with 22·9 per cent., shown in specimen No. 12.

For the totals, the highest one obtained is in the case of the left-side wing with 23·8 per cent., as against one of only 17·1 on the other side.

An analysis for the different portions of the two wings, however, gives the general

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result of an even balance for the specimens as a whole, as may be seen by the following figures :—

	Higher °/₀ losses.			
	Left side.	Right side.	Equal °/₀ loss.	Total.
Metacarpo-digitals	8 specimens.	10 specimens.	9 specimens.	27 specimens.
Cubitals	10 „	10 „	7 „	27 „
Composite wing	11 „	12 „	4 „	27 „

Perfect symmetry is present only in four specimens ; these are Nos. 4, 14, 22, and 25. For greatest differences of asymmetry amongst these specimens the numbers are distributed as follows :—

For the *metacarpo-digitals*, two out of ten specimens, namely, one each (for each side of the wing). These are Nos. 9 and 24.

For the *cubitals*, one out of 15 (for the left side). This is No. 10.

These differences get considerably levelled in their aggregates, as may be seen from the *totals* obtained between the left and the right wing of Nos. 8 and 10, which two specimens show the amount of this difference to be one of 7 per cent. for each.

Finally, as indicated in the column of percentages of the total feather-loss for both wings (see grand totals), this does not exceed ½ of all the flight-feathers, as specimen No. 10 shows, with the highest total of all, viz. 20·1 per cent.

E. *The Wing-coverts.* Tectrices primæ serii *s.* majores.

1. *Superiores.*

The upper major coverts are usually the most prominent ones of the series which accompany the flight-feathers, and to which they are more closely related than are any of the remaining series. They also resemble flight-feathers entirely, both in texture and development. When fully developed, their length on the manus is about one-third part of each flight-feather in this species.

On the cubital portion these coverts are proportionately longer, covering about one-half of their respective remiges. But whilst the latter maintain a nearly uniform length as far as remex VII., from whence to the last or remex X. they rapidly decrease in length, their upper major coverts, on the contrary, slightly increase in length in the same direction, *i. e.* towards the upper arm.

In the flexion of the wing known as the carpal joint, the first covert belonging to the hand and the first one belonging to the cubital portion, which are directly approximated here, are of nearly equal lengths, as are also their respective flight-feathers.

Metacarpo-digital portion.—The order in which the dorsal major coverts make their appearance on the manus is precisely the same as that of the remiges, being one of perfect synchronism both for growth as well as for the respective sequence of renewal. I have never found any deviation from this principle in the normally developed

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individuals which I have examined. Whenever I met with any exception it happened only where the remex in moult had been accidentally retarded in growth. The latter case can invariably be detected from the normal course of development which the major covert pursues, provided that the anomaly has not been caused by external injury.

Now and then the allied covert is shed a little in advance of its remex, but in the majority of individuals it is shed simultaneously with it. Only in three cases did I find the conditions reversed—that is, the remex preceding the principal dorsal covert in moult by being shed first.

The rule therefore of the dorsal major coverts slightly preceding in moult their respectively accompanying flight-feathers is a character inherent to the conditions prevailing for the acquisition of the first or plumage of the fledgling bird.

This law being so uniformly carried out as regards the metacarpo-digital portion, a few remarks, having reference to the alleged *undecem-pennate* forms of Passerine birds of Gadow (21), may be made here.

So long as it was taken for granted generally that the main covert directly associated with a quill was the one which lies proximad to the latter, it follows that Dr. Gadow was without question fully entitled to the conclusions he had then arrived at in regard to the exact relationship of the terminal feathers. But, when inquiring later into this matter (Degen (16), pp. x–xiii), I was able to show histologically, as well as by means of the physiological conditions of moult (see also figures 2 & 3, *l. c.*), that the conditions were invariably reversed, viz., that the major coverts most intimately connected with the main quills were those which are lying *distad* to the latter. This naturally had the effect of leaving one feather less to be disposed of, instead of the two supernumerary ones as in the case of Dr. Gadow (his alleged 11th quill and its corresponding covert), for a great number of genera and species of *Passeres*; those with 9 and those with 10 primaries alike, including amongst the latter also the species under special consideration. Dr. Gadow's own words (pp. 659 & 660, *l. c.*) on this point are:—"In some cases there might be some doubt whether the little terminal feather in question is really a primary, but this can easily be settled by the presence of the corresponding upper coverts. Moreover, *there are many cases in which the primary is still longer than its covert*[1]. When the 10th or 11th quill is much shortened, *the corresponding lower covert is absent in the Passeres*[1]. The *Alaudidæ* prove that the 10th quill is capable of being shifted dorsalwards, so that it becomes enclosed between the outer vane of the 9th primary and the 10th upper covert, instead of being freely visible below and in front of the 9th primary; when seen from below, it is hidden by the outer vane of the 9th primary. This shifting explains the conditions which are the rule amongst the birds of Group D (p. 664, *l. c.*). *The 11th primary undergoes a similar dislocation in a more marked degree*"[1].

[1] These *italics* are mine.

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In agreement, then, with the issue of flight-feathers on the hand-portion of the wing, if the terminal feather in question were a primary, it follows that, like the remainder, it should moult in turn, after the renewal of remex X. Such, however, is not the case, as specimen No. 24—the only one showing this stage—proves. On the right wing of the latter this feather has been renewed, whilst remex X. is still the old one, and its own major covert, recently shed, lying distad to it as previously explained, is just emerging, showing the apex of the new growth, anticipatory of the shedding of remex X. itself. This particular stage of moult is slightly in arrear on the left-side wing of this specimen, the general conditions being otherwise quite similar. Here, however, instead of this alleged primary being renewed already (it proved to be the old one yet by accidentally dropping out upon being touched, which is a sure sign of its impending renewal) before the covert belonging to primary X., the old one was not yet shed. There is consequently a strong probability in favour of this terminal feather being the major covert belonging to the ventral series (median ?) of the suppressed remex XI. (*remicle*), by its moulting in advance of the remiges, a condition which does apply to the ventral series, as we shall see further on when considering their moult.

Cubital Portion.—The conditions under which these major coverts issue differ so widely from those previously dealt with that they are well deserving of more careful consideration.

Whilst there is the same unalterable mode of renewal retained for this series of feathers on the manus throughout all subsequent periods of general moult by repeating the first mode of acquisition, such is not the case for the major coverts of the cubital portion.

Here we are confronted by the occurrence of several transitory stages between birds of the first season and those of subsequent ages. Broadly speaking, there are three different stages conspicuous [1], which may be further subdivided as follows :—

Stage I. Condition of renewal for Bird of second season.

(*a*) Growth of major coverts (0) 1–7 simultaneous (0 representing carpal covert).

(*b*) Growth of coverts 8–10 consecutive in the order of these numerals forming Group 1.

Following upon the mode of the renewal of the first season's bird or fledgling stage, which consisted of the simultaneous growth of the whole series of these coverts from 1–10, the mode of the first perennial moult differs by coverts 8, 9, 10 constituting themselves into a definite group. Specimen No. 4 represents this first stage in a striking manner on both wings (*cf.* fig. 1, Table IV.). The major coverts 8–10 are differentiated from those of 1–7, which are all of uniform length in development, by

[1] This refers to renewal only, and does not include the initial stage of feathering of the fledgling.

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being graduated in length of growth, a condition which corresponds with that of their corresponding flight-feathers. This first grouping arrangement is well defined in all the specimens of birds of the second season and upwards.

STAGE II. Group-moulting of various degrees of development.

1. Consisting of formation of previous Group (I.) with the remainder of coverts (0–7) renewing from 7–1 (0) in outward direction. (See Table IV. fig. 1.)
2. Consists of coverts (0) 1–4, or Group II., renewing in an inward direction. All the feathers of this second group are either equal in length or partly in graduated condition of development. In the latter case they are supplied from without inwards. (See Table IV. fig. 2.)
3. Consists of coverts 5–7, forming Group III. The feathers belonging to this third group at this stage appear still simultaneously (*cf.* diagr. Table IV. fig. 3). (Feathers in nascent condition of development.)

The first degree is common to all individuals, both young and old, and particularly clearly defined for Group I. in specimen No. 4, as quoted already. (Table IV. fig. 1.)

The second degree is represented by specimen No. 2, more particularly so for the right wing; by No. 6, left side; and No. 14 on both sides. (*Cf.* Table IV. figs. 2, 3.)

The third degree of this stage of moult, represented in diagram by specimen No. 19 (see Table IV. fig. 3), occurs on right side of specimen No. 5, both sides of Nos. 9 and 15, and on the right-side wing of No. 23. In the latter specimen we have a remarkable combination of two cases of transition from one stage to another by its left-side wing already adopting the more advanced condition of the fully adult individuals of the last, or

STAGE III. In which the main dorsal coverts follow the same perfected group-arrangement of moulting in synchronism and in the identical order of appearance as their respective remiges. This condition is shown in the diagrams by specimen No. 24. (See Table IV. fig. 4.)

This last stage is achieved only by the oldest individuals, and is attained by the metamorphic steps of consecutive moults, commencing with the young and finishing with the fully matured bird.

Further examples of this latter kind are to be seen on the left side of No. 21, an adult male, in which the carpals and coverts 1 and 2 have been completed, as have their respective remiges. Coverts 3 and 4 are equally incomplete as are these remiges. This condition obtains independently and in addition to the renewal of coverts 8–10 as a first definite group. On the left side of No. 23, a young female, we have, besides the same independent final formation of Group I., the incomplete growth of coverts 3 and 4, which, though slightly in advance of growth as compared with the other side, is proportionate to that of their equally incomplete remiges; whilst at this stage,

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covert 7, which is in a nascent condition of growth, foreshadows the impending moult of the remex with which it is associated. Coverts 5 and 6 appear to be the old feathers as yet unaffected by moult.

There is no necessity to dwell in detail upon all the remaining old individuals, as they obey the law stated in the cases quoted above, which is that of perfected group-moulting as it applies to the flight-feathers which occupy the cubital portion of the wing.

Unlike the well-defined synchronism with which the upper major coverts keep pace with the remiges of the hand-portion, there exists a marked contrast in the way they make their appearance on the forearm, inasmuch as they follow the general tendency for moulting in advance of their allied remiges, irrespective of age. Through some inexplicable agency, and for a much longer period—in fact, through nearly every moult during the bird's life,—they adhere to the more primitive conditions of the first, or fledgling livery. The only admissible inference to be drawn from this fact must be one largely in favour of this early endowment of wing-feathers to be a secondary provision and of ontogenetic origin.

2. *Inferiores.*

Metacarpo-digital Portion.—The difficulties in following up the order of renewal which this series adopts are greater than those attending the researches into the previously considered upper series. The chief one arises from the circumstance of the more protected position which they occupy on the inner side of the wing, and in which they suffer less from the effects of wear than feathers which are constantly exposed. Hence the greater difficulty for determining between old and new growth in fully developed feathers. It is only when particles of the capsule within which they were formed are still adhering to the recently renewed feather that the fact can be ascertained, or where the renewal consists of feathers in a state of nascent growth. We cannot expect to meet with the latter phase in any considerable number of individuals alike, and therefore I could find positive evidence on this head only in 9 birds out of 25 specimens after deducting Nos. 26–32, which are in a state of actually complete renewal or nearly so.

With one exception only, viz., that of the old female No. 22, these specimens are characterized by almost perfect bilateralism of symmetry on the two wings as regards the hand-portion for the moult of this series of coverts. These are Nos. 1, 14, 16, 17, 18, 19, 20, 22, 24, and 25. According to their ages and sexes they range as follows:—

		Totals.
Males.	Old: Nos. 1, 17, 18, 20, 24, 25	6
„	Young: No. 16	1
Females.	Old: No. 22	1
„	Young: Nos. 14, 19	2

By leaving out from immediate consideration the old male No. 1, obtained in the

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first batch of Nov. 5, with Nos. 2 and 3, it is noticeable that, of the birds received before the dates of December 11 and 19, which are represented by specimens Nos. 14 and 16 respectively, none exhibit any signs of moult having set in for this row of coverts. Nearly all of these represent young birds, and there is good reason for assuming that Nos. 9 and 10 are not fully adult either, as I considered them to be at that time, judging from external appearance alone. It is therefore evident that the renewal of this row amongst younger birds does not set in until about towards the middle of the period of perennial moult.

The renewal of this series takes place in the same order as that of their respective remiges and upper major coverts, which commences with the innermost and concludes with the 10th or outermost, though differing in regard to chronicism according to age.

In the youngest birds no lower major covert is renewed until nearly six to eight flight-feathers have been formed. From this retarded appearance every subsequent moult recovers one or two places from the flight-feathers which moult in advance of them, till, finally, in the perfectly adult stage, their renewal synchronizes absolutely with that of the flight-feather with which they are associated.

The most instructive specimen on the list, representing this culminating phase, is that of the old male No. 1 (see Table IV. fig. 6), which is also one of the earliest for beginning the moult for this series of feathers. Its remiges I. and II., together with their dorsal major coverts, which under all circumstances are the earliest to moult, are simultaneously accompanied in moult by their respective ventral major coverts. Indeed, on its left side, the inferior covert 3 is slightly in advance for making its appearance of the old remex III., which, having just been shed off, shows no sign yet of the new-growth quill. The same condition obtains for the remiges on the right side of the wing, the inferior coverts 1 and 2 being synchronous with the dorsal ones, which are being renewed also at this stage.

The adult male No. 25 is similarly characteristic for almost perfect synchronism, though No. 24, an old male too, of which a diagram has been appended (Table IV. fig. 4), represents one of the later stages of transition from the juvenile to the fully adult phase of this row in relation to the flight-feathers. Both these specimens were procured towards the end of the moulting-season, as their numbering shows, and accordingly were in a much more advanced condition of the moult.

The remaining specimens, Nos. 17–20, represent every conceivable transitory phase of retardation from their remiges by a steady progression for each moult of one ventral major covert, from their original arrear of 8 (well instanced by specimen No. 18, see diagr. Table IV. fig. 5) down to the case of absolutely simultaneous movement so characteristic of adult birds, as explained above; this is continued through every subsequent moult of the bird's life.

The diagrams on Table IV. (major coverts) for specimens Nos. 18 (fig. 5), 14 (fig. 2), 19 (fig. 3), 1 (fig. 6), and 24 (fig. 4) illustrate some of these transitory stages.

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Cubital Portion.—This row of covert-feathers being suppressed in all the Passerine birds, no positive information is available through this species for their behaviour under conditions of moult.

A provisional examination of a *diastataxic* species (*Platycercus eximius*) shows that there is no material deviation from the moult of their dorsal congeners as regards synchronism with their remiges, excepting perhaps that they exhibit a tendency to moult somewhat earlier than the latter and also adhere to the juvenile mode of simultaneous replacement through more than one perennial change.

Tectrices secundæ serii *or* Tectrices mediæ.

1. *Superiores.*

Metacarpo-digital Portion.—In striking contrast to the order of the moult which is adopted by the first series of satellites in relation to the remiges, stands that of the second series, or the medians.

In the former, as we have seen, it consisted in a rhythmical accompaniment to their remiges in the order of the growth of the latter. Not so for the dorsal median coverts. *Their renewal proceeds from two separate points on this portion of the wing.*

The first of these two points, the earlier one at which moult sets in, is identical with remex I. and its upper major covert. Its moult, however, does not synchronize with these, because the earliest signs of moult of median coverts do not appear until after the renewal of from 4–5 remiges with their principal satellites has taken place.

The second point at which moult sets in on the manus coincides with remex VII., and proceeds in the same outward direction as does that from the proximal centre.

This different mode of renewal therefore bisects the hand-portion into two areas: a first or proximal one comprising median coverts 1–6, and a second or distad section made up by coverts 7–10. In birds at the beginning of the moult, and in which not more than from 2–4 remiges are in process of renewal, as yet no medians make their appearance.

The earliest specimen on the list in which the first and innermost of median coverts is being formed is No. 3 on its right-side wing, which has reached the stage of *e* (see also Diagr. B, Plate XXXVI., right side), or the moult of remex V. The next specimen is No. 6, on the right side, too, of which median coverts 1 and 2 are in course of formation. Its stage of development for remiges is the same as that of the previous specimen, viz. that of remex V., which denotes a slightly more advanced condition here. This specimen, moreover, has reached a more advanced condition on its left side, where median covert 3 is being renewed also. The renewal of 3 median coverts, however, generally coincides with that of remex VI., which is the more normal course which these coverts pursue. This is well defined on the right side of No. 9.

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EXPLANATION OF TABLE IV.

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The letters **M.C.D.** or **C.**, placed above each diagram, signify *Metacarpo-digitals* or *Cubitals*.

The Roman cyphers, from I. to X., above the symbols ○ ○ &c. of figure 1, denote the numerical order of the remiges and the major coverts, with which they are allied, and apply also to the other diagrams beneath.

The darts placed over or below any sub-series of major coverts point in the direction of their respective sequence of moult.

The spherical symbols (and further explained on table itself) represent a theoretical cross-section through the projected quills and coverts for which they stand, made longitudinally the whole length of the posterior margin of the extended wing, or portion of it, as in the case of figs. 5 & 6.

Fig. 1. Showing Group-moulting for the upper major coverts VIII.–X. on the cubitus, and the simultaneous appearance for I.–VII. in relation to their remiges under moult (Degree 1). Also showing the relative movement of the remiges and the major coverts for the hand-portion.

Fig. 2. Shows upper cubital major coverts I.–IV. inclusive of carpal covert, forming Group II. by moulting in an inward direction, or one opposed to the stage for the same sub-series, illustrated in specimen represented by fig. 1. It further shows the first stage of moult in relationship to the remiges of the inferior major coverts for the hand-portion (2nd degree).

Fig. 3. Shows the 3rd degree, or that of cubital major coverts V.–VII., constituting Group III., its integers as yet appearing simultaneously. It also shows the more advanced condition of moult for the progressive movement of the ventral major coverts on the hand-portion of the wing.

Fig. 4. Shows the final stage of moult in their relationship to each other of the remiges and the major coverts, both upper and lower, in synchronous Group-arrangement for the cubitus, and in regular sequence outwards for the metacarpo-digital portion, a mode which is adopted only by the fully adult bird.

Fig. 5. Shows the initial stage in the replacement of the inferior major coverts for the hand-portion.

Fig. 6. Represents a similar stage, though slightly in advance of that seen in fig. 5.

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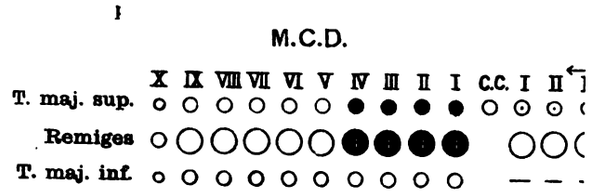
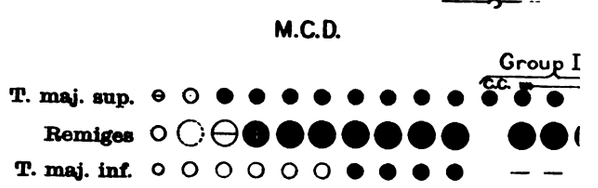
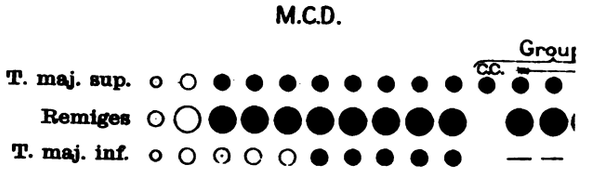
Stage I

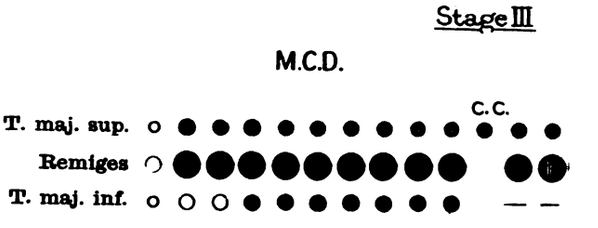


Stage II





Stage III



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The renewal of median covert 4, which is the next stage, as a rule corresponds with that of remiges VI. and VII. To this condition, specimens Nos. 7 (right side), 10 (both sides), 11 (both sides), and also 15 testify very clearly.

At this stage the 5th median covert is frequently shed also, preparatory for its speedy replacement, though in the majority of cases its moult corresponds with that of primary VII., as does also median covert 6, whose moult rapidly follows that of the 5th of this series.

The morphological features for the coverts of the outer section, or distad area, are as follows:—Dorsal median-covert 7 is renewed when the synonymous coverts 2 and 3 of the inner section are formed—that is to say, in advance by one place of remiges V. and VI. under moult (see diagr. Table V. fig. 1, referring to right side of specimen No. 5). Synchronous with the formation of medians 1–4, the 8th also follows on in rapid succession to the 7th. This is well marked in specimens Nos. 7 (Table V. fig. 2 of diagr.) and 10 (both on right side). At the time of the formation of medians 5 and 6, the last two to moult of the proximal area, the 9th and the 10th or last coverts of the distal area are also developed in rapid succession of each other. This phase corresponds with that constituting the renewal of remex VIII.

In this manner, then, the moult of the medians forming the outer section is invariably accomplished considerably in advance of their corresponding remiges VIII., IX., and X. This is particularly noticeable in those specimens which partake of the later stages of the perennial moult. These are Nos. 15–24, but especially is this the case in No. 11 with its 5th covert just shed, and which, by still retaining the old covert 6 on the right, also shows coverts 7, 8, 9, and 10 in a state of complete renewal. This typical case for the relative position of the moult of these coverts is seen in the diagrams of Table V. specimen No. 7 (fig. 2) and No. 11 (fig. 3).

In birds of the season, however, the mode of renewal for the feathers of this series is a simultaneous one still, the same as it is for the fledgling. This is seen in Nos. 2, 12, and 14—birds which are undergoing their first autumn moult in the season in which they were hatched. Specimen No. 12 in Table V. fig. 4 shows this particular condition.

Cubital Portion.—The median coverts of this portion of the wing evince a strong tendency not only for keeping pace with the moult of their respective remiges, but actually preceding them, though not to such an extent as in the case of the major coverts, of which latter they are, therefore, in arrear. This is not only noticeable in the case of the young individuals to which the embryonic condition for simultaneous moulting applies, analogous to that of the major coverts, but a similarly accelerated appearance of this series is seen to take place when the series is broken up, in order to moult in groups, which is the ultimate adoption of renewal in the mature bird. The transition from the former to the latter is effected by various intermediary stages, which lead up to the same grouping-system as that of the remiges, viz. their subsequent alternate direction of moult.

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In the majority of the specimens the growth of these coverts proceeds in a fairly symmetrical manner from both wings for either of the two systems of moult. It, however, happens frequently, notably in the younger birds, that while the juvenile mode is prevailing still on the one wing, the other wing may have already adopted a stage of the later conditions.

Instances of perfect symmetry for the earlier stage of simultaneous development of the series are Nos. 5, 12, and 15, which are all young birds; while a case of dualism of development occurs, amongst others, in No. 13. In this latter specimen the wing of the left-side is still following the early principle of simultaneous replacement; it is marked in this case by uniformity in length of all its coverts which constitute this co-series; whereas on the right side, while still repeating the early mode on the proximal portion of the cubitus from the 5th covert to the 10th (including a slight modification of the 8th), the mode of the first definite formation for moulting in groups has taken place on its distal part for coverts 1–4. This is shown by the diminishing lengths in development of these coverts in their inward numerical order.

In reference to the modification of covert 8, as alluded to above, it is not a little curious to find this covert to be the only one in a nascent state of growth amongst those from 6–10, which are all about half-grown. Herein, then, we have an early indication of plainly denoting the initial point in the ultimate formation of the first group, which comprises coverts 8, 9, and 10. This arrangement corresponds exactly with that of the issue of the remiges and the main coverts in this place which have preceded them in development.

Illustrations of perfect conditions for the group-moulting are Nos. 3 (left side), 11 (both sides), 13 (right side), 16 (right side), and probably all the remainder of adults in which the moult of this co-series had been positively completed at the time of their reception.

2. *Inferiores.*

Metacarpo-digital Portion.—Quite distinct from the mode of renewal by means of two separate sections of their dorsal congeners at a comparatively immature age, the set of coverts under consideration here *apparently* follows the rule which applies to the remiges and the main coverts of the young individual undergoing its first autumn moult, viz. in the ordinal appearance of the feathers from 1–10.

The main cause for this *apparent*[1] difference lies in the fact that they begin to moult later than their companion coverts of the dorsal series; but this is a delusion only. It is not until from three to four of the latter have emerged and are fairly developed that the first ventral median begins to replace its old feather. The others follow suit in rapid succession, completing the inner section with the 6th, and so reach the 7th covert or first of the outer section at about the same time as this latter emerges from the skin. This arrangement gives it the appearance of a continuous growth for the whole series, and *therefore produces* the *delusion* referred to before.

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Fortunately, among the specimens procured to supply data for the various stages, No. 15 provides us with the desired information on the subject, where *medeæ inferiores* 1, 2, and 3 of the inner area, and 7, 8, 9, and 10, belonging to the outer one, are in course of renewal. That it is not a merely accidental circumstance, but a reliable case, is further evidenced by the perfect symmetry of the occurrence on both wings.

The relative position for the renewal of the ventral series in the juv. ♂, specimen 15, to their dorsal congeners (see diagram of Table V. fig. 5) can be adequately formulated thus:—

Metacarpo-digital Portion.

	Left wing.		Right wing.	
	Distal area.	Proximal area.	Proximal area.	Distal area.
Dorsal series . . .	10, 9, 8, 7, ——	4, 3, 2, 1	1, 2, 3, (4)°, (5)°, —	7, 8, 9, 10
Ventral series . . .	10, 9, 8, 7, ———	3, 2, 1	1, 2, 3, ———	7, 8, 9, 10

The symbol °, placed above figures 4 and 5 of the coverts of the dorsal series of the right side, denotes that these feathers were recently shed, thus showing the relative movement for the different constituents of this row to be in nearly perfect synchronism within the two areas; whereas for the left wing the 4th covert of the dorsal row, having been replaced already, constitutes a case of retardation for the proximal area, the old covert 5 being still retained.

However, individuals older by a season or two acquire perfect conditions of synchronism for the dorsal and ventral rows within the same area, and a highly instructive example of this is seen in the old male No. 10 (see also Table V. fig. 6), which, moreover, shows the connection of the moult between the inner and the outer area for the *ventral* medians, as below:—

Metacarpo-digital Portion.

	Left wing.		Right wing.	
	Distal area.	Proximal area.	Proximal area.	Distal area.
Dorsal series . . .	—— 9, 8, 7, ——	(4)°, 3, 2, 1	1, 2, 3, 4, ———	7, 8, ——
Ventral series . .	———	(8)°, 7, (6)°, 5, 4, 3, 2, 1	1, 2, 3, 4, 5, ——	7, 8, ——

It may be seen from the above formula that there is a slight overbalance of synchronism in favour of the first division for the *ventrals* in the shape of covert 5 on the right side, and, in addition to this covert 5, on the left by the 6th covert being shed preparatory to its immediate renewal. This sectional synchronism can be studied only on those few specimens which represent individuals of middle age, combining with the latter requisite that also of this particular phase of the perennial moult. In the specimens procured at a later period, the moult of this series is invariably completed throughout.

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During the first total feather-change in the young bird, and to a great extent also in that of the following season, all the feathers constituting this series make their appearance simultaneously and parallel with the dorsal row of medians 1–10, without the ultimate division into the metacarpal and the digital area, which is so characteristic for subsequent moults. In this case, however, the synchronous development with their equivalents of the dorsal series is a perfect one in their entirety. Partly in the second, but wholly so in the third season, the transitory step from the one mode to the other is effected by an intermediary stage. This consists in the inferior row moulting in arrear of the dorsal one still, while yet adhering to the non-deciduous form of renewal by means of a gradual supply of the feathers which begins with covert 1 (the innermost) and ends with 10 (the outermost). The dorsal row has meanwhile already acquired, either on one side only or symmetrically from both wings, the perennial or deciduous style above mentioned of the areal form of moult.

Nos. 7, 8, 11, 12 (see also diagrams for these, Table V. figs. 3 & 4), and also 13 are examples of specimens of either one or the other of these transitory cases. The fully adult mode of moult, in which the ventral equivalents are renewed in absolute synchronism with the dorsals, is reached only when the bird attains the positively adult stage, and not before the 4th annual moult.

An approximate key to the various phases of the relative development between the dorsal and ventral rows is appended at the close of the description for the whole of these series (see p. 390).

Cubital Portion.—Bilateral symmetry, as we have seen it to exist mainly for the hand-portion of the wing, is not nearly so pronounced a feature on the forearm for this row of feathers. Out of 10 specimens showing this phase of the moult there are 3 which show cases of asymmetry in the corresponding portions of the two wings, as the following analysis of these specimens shows:—

Symmetrical Development.

Males.	Old: Nos. 17, 20, 24, 25	4	
„	Young	—	
Females.	Old	—	
„	Young: Nos. 14, 19, 23	3	
	Total . .	—	7

Asymmetrical Development.

Males.	Old: No. 1	1	
„	Young: No. 4	1	
Females.	Old	—	
„	Young: No. 12	1	
	Total . .	—	3
	Grand total		10

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EXPLANATION OF TABLE V.

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T. med. sup. = Tectrices mediæ superiores.
T. med. inf. = Tectrices mediæ inferiores.
Cyphers, symbols, and other abbreviations similar to those used in Table IV.

Fig. 1. Metacarpo-digital portion of right-side wing, showing the moult of medians I. and II., and the first to appear of the proximal section. Also median VII., the first covert of the distal section.
No inferior medians in moult at this stage.

Fig. 2. Metacarpo-digital portion of right-side wing, showing the more advanced condition of four medians belonging to the proximal section in moult, and two, medians VII. and VIII., on distal section.
Inferior medians I., II., and III. in moult also at this stage.

Fig. 3. Metacarpo-digital portion of right-side wing, showing dorsal median V. of proximal section as the next in turn, shed off, preparatory for its replacement by new feather.
All the coverts of this series belonging to the outer section are replaced, also the whole series of the ventral or inferior medians.

Fig. 4. Metacarpo-digital portion of right-side wing, showing the renewal of the dorsal medians in regular sequence of their ordinal numbers, irrespective of the two sections, and a typical instance of the perennial moult of a first season's bird.

Fig. 5. Metacarpo-digital portion of left- and right-side wing.
In this the sub-serial renewal for the two sections may be seen; both for their chronicism between the dorsal and the ventral series of medians, as it takes place in a younger individual.

Fig. 6. Left- and right-side metacarpo-digital portions of the wing, also showing the chronological renewal of these series in the case of the fully adult individual.

Fig. 7. Cubital portion of the right-side wing.
Principally shows the mode of renewal for the inferior medians in the very young bird in their consecutive order for the whole series towards the wrist-joint from X.–I.

Fig. 8. Cubital portion of right-side wing, by specimen showing the typical condition of the moult of the dorsal medians in advance of the remiges.
Also showing first signs of Group-moulting for the inferior row, in which coverts I. and II. belonging to Group II. moult in opposite or inward direction.

Fig. 9. Cubital portion of right-side wing, showing more advanced condition of previous diagram by 4 inferior medians being in progressive stages of growth, also in inward direction of moult; while those of group I., or medians X., IX., & VIII., are as yet adhering to the conditions of the moult of the fledgling bird, *i. e.* by moulting in an outward direction.

Fig. 10. Cubital portion of the left wing.
This is an example of the final phase in the replacement of the inferior median coverts, and shows the ultimate grouping-arrangement with directions of moult—inwards for Groups I. & II., outwards for the middle or Group III.

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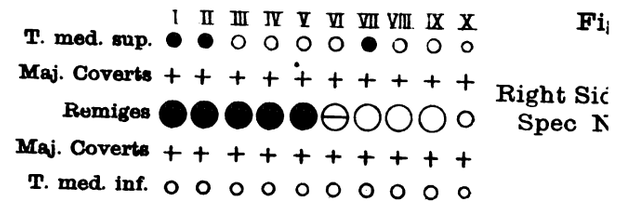

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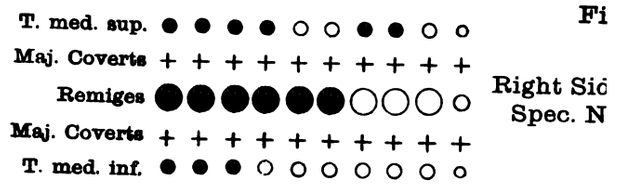

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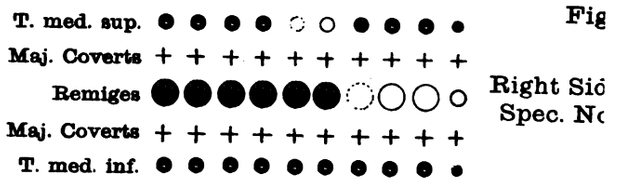

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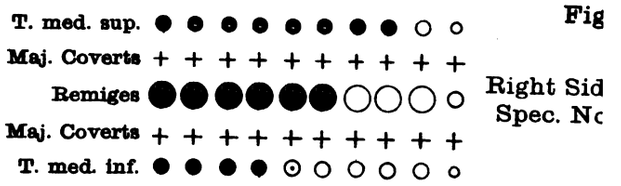

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Various phases from the Moult of the M
Coverts on Metacarpo-Digital Portion of W

Meta

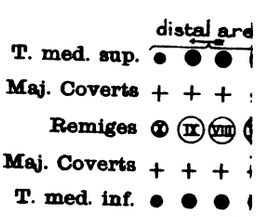

Fig. 5.

L

Meta

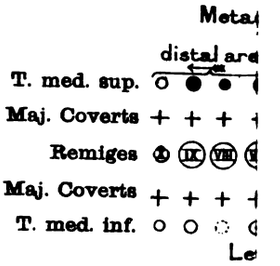

Fig. 6.

L

E. Degen, del.

Diagrams explaining
Median Coverts fo

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The moult of these inferior medians, moreover, appears to be more erratic than is the case for the corresponding dorsal row of coverts. Besides this there exists a strong tendency to adhere to the conditions of the first endowment, in which the whole series is provided by a gradual advance of the growth from the elbow- towards the wrist-joint. The young female, No. 14 (see diagram Table V. fig. 7), is a particularly typical case of such a repetition of conditions, and so also is No. 4, a younger female still, as regards its left side only.

It is not, therefore, until the more matured specimens are consulted that the same plan as the one ascribed to their dorsal companion-coverts will be found to have been resorted to, namely, the moulting of the feathers within the groups in distinctly alternate directions. Even this, their ultimate order of perfect synchronism of movement with their respective remiges and major coverts, is not achieved by any but positively old birds, and that tendency to retardation, as referred to above, prevails for a considerably longer period of the bird's lifetime. The diagrams for the specimens of Table V. figs. 7–10 further supplement the explanation given above for the relative position of the ventral to the dorsal median coverts.

This conservative tendency is fully borne out by specimen No. 17 (Table V. fig. 8), which, although being entitled in other respects to be put down as an old male, has, nevertheless, only four of these coverts renewed in proportion to the eight cubital remiges on both wings; these are inner coverts 9 and 10, and the outer coverts 1 and 2. No. 20, too, with the same number of remiges renewed already as No. 17 (the previous specimen), has only two of these coverts in moult.

This tenacity to adhere to the juvenile conditions of growth is carried far within the grouping arrangement also in No. 11 (Table V. fig. 9), in which it is adhered to in the first group, comprising coverts 8–10, whose numbers instead of being renewed in this, their ultimate numerical order, are being still renewed in inverse order—that is, from 10 to 8, as they would be in a bird of the first season's plumage. On the other hand, this same individual shows for coverts 1, 2, 3, and 4 (inclusive of the carpal covert), which form the members of group 2, all the conditions followed by a bird of a more advanced stage, by beginning the moult from the carpal joint to the 4th, *i. e.* from the wrist towards the middle. The old males, Nos. 24 (see also diagr., Table V. fig. 10) and 25, approach the conditions of perfect synchronous development with their flight-feathers; and, further, the old male No. 1 equally bears reliable testimony on its left side for inferior median covert 8 being the first to be renewed, together with its corresponding main quill.

In addition to the remarks made above on the subject of bilateral symmetry, it should be pointed out that not only are cases of asymmetry more numerous when compared with the corresponding two cubital portions of the wing, but also for their hand-portions. Thus, in old males three out of a total of eleven are asymmetrical;

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young males one of two; also the single old female which represents the moult of this series is asymmetrical for the metacarpo-digital portion; and of the four young females three are similarly affected.

Tectrices tertiæ serii *s.* minores.

1. *Superiores.*

Although this series of coverts is of minor importance to the flight-power of the wing, the manner in which they moult is of some morphological consequence.

Metacarpo-digital Portion.—On the manus the dorsal coverts of this series frequently precede in moult the other satellites. This they generally do in the same order as those of the higher series. But, as happens sometimes in the case of their cubital equivalents, several of them make their appearance simultaneously. They are unimportant for the covering of this part and of abortive growth.

Cubital Portion.—Here these coverts are confined to a single row also. The typical manner in which they are renewed imparts to them a special morphological feature, which is of some value as regards the definition of the different series.

Their moult differs markedly from their neighbouring rows of "marginal coverts" on the patagium and of the true covert-feathers whose description has already been given.

Their moult consists in a successive supply which begins with the innermost—contemporaneously almost with that of the feathers constituting the "parapterum," which latter in its turn follows that of the "humeral tract,"—and ends with the outermost. The coverts of this series do not take part in the grouping arrangement which is so characteristic a feature in the major coverts and the medians—not even in the fully adult.

The tendency for simultaneous development of three and four feathers is very prominent, and prevails more or less in every perennial moult. Whenever such is the case, it invariably takes place from within outwards, viz. the 10th to the 1st.

Furthermore, this mode of renewal distinguishes the row from the marginal series, whose renewal, although following the same outward direction generally, takes place in patches which begin on the anterior edge of the patagium, whence it spreads over both the dorsal and the ventral side of the wing in such a way that the several longitudinal rows are diagonally affected at the same time.

Thus it is through the agency of the moult principally that their morphological character as a row of covert-feathers can be equally established as being derived from a different source than either the higher series or the marginals. Where, as for instance in the more primitive forms of birds, the minors consist of several rows, these are generally made conspicuous by reversed overlap, a feature which has so greatly engaged the attention of Mr. Goodchild (27).

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2. *Inferiores.*

Metacarpo-digital Portion.—The feathers which constitute this series of minors are of such abortive growth that they are practically of no value for the covering of this part, and, as a consequence, no information is available with regard to the order of their renewal.

Cubital Portion.—The feathers of this row, not so much on account of their diminutive size (being scarcely $\frac{2}{3}$ the length of the medians), but because of the method of their renewal, are well worthy of a more special consideration.

It would seem that, with the suppression of the major coverts on the underside of the wing in the Passeres, the physiological functions of the latter had been transferred to the next row, viz. the medians, and in the same way that of the medians to the minors. Both these series have their moult more accentuated and more in keeping with that of the higher equivalents of the dorsal surface.

The first appearance of the members of this co-series is somewhat earlier than that of their dorsal congeners in the very young bird. In Nos. 7, 8, and 9, for instance, all very young individuals and of early dates, this row moults in advance of the dorsal one. Singularly enough, in the three specimens mentioned, the renewal begins at the carpal flexion, and proceeds inwards, which is in an opposite direction to the renewal of the dorsal series. This fact therefore foreshadows the ultimate method of moulting in groups, and is significant.

Specimens 5, 11, and 12 are examples of the earliest, or caducous, mode, in which the inferior row is developed strictly in synchrony with the members of the dorsal row. No. 12 makes an exception, perhaps, so far that the coverts of the inferior row are all in a nascent state only, and they are consequently in arrear of those of the dorsal row, whose components have developed $\frac{2}{3}$ of their ultimate length, and symmetrically from the two wings.

The transition from the premature to the fully mature condition of moult is a very erratic one for the whole series. In the few specimens, however, which show such evidence of transition, as, for instance, Nos. 13 (both sides), 15 (right side only), and 16 (left side), group-moulting sets in first, sometimes for the proximal, sometimes for the distal group, and in one case contemporaneously for both these groups; whilst the middle group, consisting of coverts 7, 6, and 5, does not appear to be affected until much later.

In any case, asymmetry seems to be a conspicuous feature in the replacement of this set for the individuals undergoing transition from the juvenile to the mature conditions of the moult. The coverts of this, as well as those of the dorsal series of minors which are allied to the remiges of group III., namely 7–5—*the last to change in every case,*—moult in advance of the latter. This is well seen in all the specimens

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from Nos. 17–23, neither of these individuals having as yet acquired remiges IV., V., and VI.

Approximate Tabular Arrangement showing the Development for the Dorsal and the Ventral Series of "Median Coverts" during four consecutive Perennial Moults.

		Rows.	Groups.	Sets.	
Supply	Simultaneous	1st	2nd–4th	1st	Season.
	Gradual	2nd–4th	1st–2nd	2nd–4th	,,
Movement	Anachronous	1st–2nd	1st–3rd	1st–3rd	,,
	Synchronous	3rd–4th	3rd–4th	3rd–4th	,,
Development	Asymmetric	1st–2nd	2nd–3rd	1st–3rd	,,
	Symmetric	2nd–4th	4th	4th	,,

VII.—Summary of the Order in the Perennial Moult of the Wing-feathers.

The Remiges.

Two distinctly different principles in the order of the shedding and eventual replacement of these feathers are conspicuous. The first is that of the regular sequence of their renewal on the hand-portion from within outwards, though accelerated in certain places or retarded in others, in order to maintain the requisite balance for flight, by a system of approximate symmetry for the whole wing during this critical change. This is the principle which forms the rule for probably the entire Order of the Passeres.

But it is by no means the expression of the real morphological process of development which takes place, as we shall have an opportunity to prove further on when studying the behaviour of the covert-feathers during the moult. The true morphological principle is probably concealed beneath this purely secondary feature. In less highly organized birds, such as the Picariæ, an earlier and more primitive mode, namely, that of starting the moult on the manus from two separate points almost simultaneously, has been observed by Wittmer Stone (44), in the case of the Kingfisher, who (on p. 112, *l. c.*), after remarking on the principle of his "Order of Molt," writes thus:—

"Following these [the two innermost primaries] the primaries are shed at short intervals, one at a time, finishing with the outermost. *Exceptions I have noticed to this order in the Belted Kingfisher*[1], *Ceryle alcyon*, and the Snow-Bunting, *Plectrophenax nivalis*"[2]. And further on (p. 113, *l. c.*):—"The Kingfisher is strikingly

[1] These *italics* are mine.

[2] Wittmer Stone, on p. 113, also quotes the case of a male *Piranga*.

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different from any other bird examined in that the *first wing-feather molted* is the *fourth primary*, followed successively by the *third*, *second*, and *first*[1]" *.

This same rule the author seems to have verified on the hand of three specimens in the same stage and coming from the same locality. But he continues :—" *How the molt proceeds*[1] after the first primary is shed, I am unable to say, *though the fifth*[1] [our VI.] is probably the next to be renewed, followed by the others in regular order inward."

It was my good fortune, when in Australia, to procure, as the first bird which I collected for this purpose, a fine specimen of a Brown Kingfisher or Laughing Jackass (*Dacelo gigas*) about the middle of the annual moult, so I am glad to be able to supplement the information desired on the point. According to my observations, the moult proceeds on the hand-portion—after having done so from the 7th outward—by immediately starting with the innermost or primary I. In the specimen observed by me this feather was nearly fully developed and further showed the *second* or next innermost in full process of moult, and the *third* cast off, preparatory for the renewal of this remex. Primary I., therefore, is the centre from which this section of the manus begins to moult next. This section comprises metacarpo-digitals I., II., III., IV., V., and VI. Although this section moults in arrear somewhat of the outer one, comprising VII., VIII., IX., X. (and XI.), yet, apart from its inner position, from a morphological point of view, it has to be considered as the first of the two.

I have elsewhere alluded to this arrangement as being overshadowed by a later principle in more specialized birds; similar signs as those referred to here for the remiges exist in some of the series of the coverts of the metacarpo-digital portion, and this is the same primitive principle as carried out more generally on the cubitus.

Gerbe (23), on p. 290, *l. c.* (see also *anteà*), was the first to point out a deviation for the forearm, from the linear progress of the moult of flight-feathers on the hand-portion; he, however, confined himself to this statement merely :—" Elle se manifest à la fois sur les deux points extrêmes du cubitus et prend deux directions qui tendent l'une vers l'autre." Beyond this he did not pursue their order of moult.

This I shall deal with in the course of my remarks on " Groups." As the initial diagrams A, B, and C show (Plate XXXVI.), the first one of these groups in which the moult sets in embraces cubital remiges VIII., IX., and X., which are renewed in the order of these numbers—that is, in a proximad direction.

Meanwhile the moult has set in also on the other extremity, beginning with cubital remex I., and by assuming the same inward direction as the group previously mentioned. This it does as far as the fourth quill, which forms the last one belonging to this group.

[1] These *italics* are mine.

* Wittmer Stone counts from the tip inwards, so that his *fourth* is probably the *seventh* (possibly the eighth in an eleven-primaried bird), after our reckoning; his *third* our *eighth*; his *second* our *ninth*; and his *first* is consequently identical with our *tenth*, at any rate last and outermost.

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The latter, which I refer to throughout as Group II. (comprising remiges I., II., III., IV.), consequently forms the other "point extrême" of which Gerbe speaks. We have disposed, then, of two groups, whose remiges severally tend in the same inward direction for their moult.

This leaves us with a balance of three flight-feathers situated between the proximad limit of Group II., viz. remex IV., and the distad limit of Group I., viz. remex VIII. The moult, however, of the remiges of this centrally situated, or Group III., *proceeds in an opposite direction* (that is, in inverse order of their numbers), namely by beginning with remex VII., then VI., and by closing it with V. In the chart (Table II.) prepared for the chronological movement of the remiges (further see diagrs., Plate XXXVI. &c.), their alternate directions of moult are indicated by darts, pointing in the respective direction of their renewal.

In this way the order of the moult of each flight-feather itself becomes a definite unit of the group to which it belongs.

Similarly, as has been explained, each group itself becomes a definite unit in the cubitus as a whole.

Consequent upon the synchronous appearance of two or more group-integers, the numerical order in the replacement of the flight-feathers within the cubital portion as a whole breaks up.

The Tectrices.

The renewal of the wing-coverts presents some notable deviations from that of the flight-feathers.

Whereas the latter adopt the ultimate plan of renewal in sections immediately in their first perennial moult, the wing-coverts do not follow this same principle so soon, except by means of a series of transitory stages. These latter form a system of complexity in which two entirely different morphological features seem to mingle with each other: the one an early horizontal or diagonally longitudinal, and the other, later one, consisting of a transversely diagonal one for renewal.

As might have been noticed, a certain amount of difficulty occurred in tracing out the two systems of development. However, in following up step by step the order of renewal of the coverts—providing an extensive series of individuals be consulted on this point—all the conditions in the physiological process of their perennial moult may be found for discriminating between the various phases which produce this state of complexity.

But in order to better comprehend the degrees of complexity attending this interesting morphological question, it has become necessary to refer to some of the statements made on the subject of those writers particularly whose works have appeared in more recent years.

The observations made by Gerbe (23) on the simultaneous shedding of the principal coverts for the hand-portion of the wing have been described fairly correctly by

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him on p. 290, *l. c.*, thus:—". . . leurs grandes couvertures qui sont pour le vol un élément important *les accompagnent toujours dans leur chute*" [1]. These researches led him also to the statement, recorded for the first time, of the two opposing directions which these coverts on the cubitus pursue for their renewal, as the flight-feathers; and further that here (on the cubital part) they are developed *in advance of their respective remiges* (see p. 290, *l. c.*).

To what extent this latter and more general statement is correct may be verified from the facts as they appeared in connection with the part dealing with these feathers. The degree of advance, as could be seen, depends upon the age of the individual. The moult of the coverts also follows the direction of the flight-feathers. This direction is not one of opposition from the extreme points of the forearm, but one which converges for the distad and the medial groups, and one which diverges for the latter and the innermost group. Gerbe did not investigate the appearance of the minor series of coverts.

Chalmers Mitchell's (12) interpretation of the longitudinal appearance of the flight-feathers and their principal coverts is that they are the co-serial members of a diagonally transverse arrangement with the other coverts, like that existing for the scaling in Reptiles, and as further diagrammatized by him in his text-figure on p. 232, *l. c.* This on p. 230 he explains thus:—

". . . . the quills and major coverts appear first as horizontal rows. It is only when these become obvious, and when one or two other longitudinal rows appear from before backwards, that the diagonal rows begin to be marked, &c."

And continuing further:—

". . . . I am not, however, prepared to attach great importance to this early ontogenetic appearance of the longitudinal rows as such."

As the result of this investigation also shows, there is in reality a marked transverse or vertical element entering into the composition. Though but faintly indicated in the chick's first perennial wing-feathering, it gradually increases with every subsequent moult by which the bird attains to perfect conditions of maturity and age. This transverse arrangement is a survival, therefore, of the phylogenetic affinities which link the present Class Aves to their Saurian ancestry.

The horizontal or longitudinal sequence of growth of the rows, applied to every series of the coverts (as well as the main quills) in their entirety, is the result of a secondary provision, and of a purely ontogenetic origin, which is assumed by the embryo and the young bird for its first set of wing-feathers.

Afterwards this same sequence of renewal becomes restricted to those sections of the rows which form part of the several groups on the forearm. Within these groups the horizontal renewal is retained throughout every moult. Each of these three sections performs this longitudinal process independently of the other two.

[1] The *italics* are mine.

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The great importance which attaches to the covert-feathers in helping to clear up outstanding questions connected with the evolution of the organ of flight was fully recognized by Mr. Pycraft (39), who has approached the subject of the origin of *Diastataxy* from the point of view of Embryology. In the course of his description of the "Embryo Wing" (see p. 239, *l. c.*) he says, for instance:—"The movement of the remiges is in all cases accompanied by a corresponding movement on the part of the coverts associated therewith, from the post- to the pre-axial border."

And continuing, he says:—"The result, when the wing is viewed as a whole, seems to show that a process of 'faulting' has taken place, &c., &c." This process of *faulting* or *shifting* he, moreover, supports by an ably devised diagram (see p. 239, *l. c.*).

It is really the first indication of a transverse rearrangement of the rows at this early stage of development. That it is a totally distinct feature from the longitudinal principle of feather-supply is equally endorsed by this author, who initiates, on p. 238, the paragraph treating of the subject by the following words:—"In all wings the feather rudiments appear first along the post-axial border of the wing; those representing the remiges and their major coverts appear simultaneously, and sometimes together with very faint traces of one or more of the pre-axial rows representing the median and minor coverts." And further:—"The change takes place, however, generally at the close of this phase of development."

Now it is this "faulting" precisely on which Goodchild in his researches has laid so much stress, and which has supplied this author with such a solid basis for his observations on the coverts of the cubitus. Further evidence of a transverse character he has clearly also shown to exist in the alternate imbrication of the members of certain series of coverts, which is so conspicuous a feature in a great number of families of birds. Similar indications of this principle may be found to exist also in the shape of the permanently shortened coverts which mark the various sections of this portion of the wing for some families of birds (Degen (16), p. xxiii). Their places almost exactly correspond with what we have learnt through the conditions under which they moult.

The appearance of a first set of wing-feather-plumage is an endowment of secondary origin. It is the common bondage for all Carinate birds. In the *Chenomorphæ*, for example, this early ontogenetic mode of feathering is repeated more or less in every moult (*anteà*, p. 366) for both portions of the wing.

In more highly organized forms, however, this latter mode is confined merely to the very young individual on the cubitus, in which, with every succeeding annual moult, the transverse character of primitive origin comes into prominence.

The latter reveals itself also by the moult of both the flight-feathers and the coverts on the metacarpo-digital portion in some families of the *Picariæ* (Kingfishers); whereas in the *Passeres*, whilst being merely concealed by a chronological difference

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for the remiges and the major coverts of this portion, it is wholly retained by the median, and in part by the minor series of coverts still, as evidenced through their moult.

VIII.—The Contour Feather-Tracts, or Pterylæ.

Preliminary Remarks.

No really so precise a description of the order which the moult pursues in these tracts is possible as that which enabled us to follow it for the "alar tracts."

One reason for this is that synchronous renewal is not circumscribed so definitely on the body as it is on the wing. But on this head I cannot do better than quote Dwight (17), whose statement, p. 84, *l. c.*, under the heading of "Advance of Moult in the Feather-Tracts," is as follows:—

"The only way to get any idea of how a moult proceeds is to appreciate the fact that it begins almost simultaneously at a number of points in the different tracts, and advances independently from each of them. This is why a bird seems to be moulting at irregular spots all over. There is, as might be expected, a good deal of individual irregularity in the growth of new feathers, *but when each tract is studied separately, each will be found to have a definite plan of development* [1], which in its turn fits into the general scheme of the process we call the moult." And, again, in connection with this subject on Gulls and Terns (18), as regards "Sequence of Moults and Plumage of the Laridæ," he says (p. 50):—

"The moults occur at definite periods, and the feather-growth spreads from definite points in the feather-tracts, so that nothing is a matter of chance unless it be the arrested development that befalls all organisms, and occasions in birds the retention of old feathers among those that are replaced by new ones at time of partial moult."

The above statements so exactly describe the conditions that exist in the species under consideration that I can add very little else to them as the result of my own investigation. In consequence, this account can be restricted to the narrowest limits by merely pointing out a few specific deviations from the broad principle.

A second reason for not being able to make a comparative survey of the moult in the various body-tracts consists in the technical difficulty presenting itself of dealing with them simultaneously, the same as they are in moult. This difficulty is further enhanced by the fact that this not only applies to the tracts themselves, but, as pointed out by Dwight (see *anteà*), to the different parts of a tract by the new growth which spreads in both a diagonal, transverse, and longitudinal mannner.

Having, moreover, early recognized the desirability to adequately express in some manner of form the complex order of moult, besides the systematic description of the different tracts, I have prepared a chart (Table VI., p. 398) as the only alternative for intelligibly conveying the relative order of their moult.

[1] The *italics* are mine.

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In this chart are entered all the tracts and the various longitudinal rows of feathers of which they consist. The rows against which an asterisk has been placed are those which form centres from which the moult proceeds. The pointed ends of the blackened bars denote approximately the beginning of moult of that particular row of feathers. The time of the completion of the moult for the same is indicated at the point where the shading reaches its maximum by filling up the space between the parallel lines which divide it from the neighbouring bar.

Beginning and completion of the moult of each row is measured by the common standard, namely, that of the development of the *Metacarpo-digital Remiges*, whose numbers in this order from right to left are placed at the head of the Table, as are also those of the *Cubitals* and the *Pennæ pollicis* for chronological comparison. A similar arrangement has been provided in this table for the rectrices and their coverts at the bottom.

The Spinal or Dorsal Tract (Pteryla spinalis).

This is of a well-defined Passerine form, and partakes of the type under which "Nitzsch" (37, pp. 79 & 80) subordinates Cuvier's Group of the Dentirostres as follows:—

"A. With 12 rectrices.

"*a.* Saddle without a space.

"1. *Barita.*—.... saddle short, broadly rhombic, acute angled. *B. strepera*, *B. destructor*, *B. varia.*"

But it also partakes in part of the description which follows for the characters applying to his second division of this group, between which it seems to fit in, namely: "2. *Thamnophilus*, seu *Vanga*, and *Lanius*, species *undulatus* and *procerus*," in which he refers to "twenty remiges which are all very broad and obtuse, graduated as far as the fifth [our VI.], which is of the same length as the sixth [V.] and seventh [IV.]." .... And further: ".... the saddle is heart-shaped reversed, emitting a single row of feathers from its middle as the commencement of the rump-band."

From this definition of the rump-band *Gymnorhina tibicen* deviates by emitting not only this single row, but two additional ones as well, whose feathers alternate by means of quinqunx from 3 to 2 for about 7 or 8 of these sets, from whence a short distance backward to the oil-gland the tract broadens further out into two more additional rows, making 5 in all.

The saddle portion itself in its widest diameter, which is placed two-thirds backward, consists of 12 rows, tapering out to 6 rows on its anterior or interscapulary portion, which further in front widens out into from 2 to 3 additional lateral rows, from which latter region it broadens out into the head tract.

I have found the moult to proceed from three distinct main centres on the principal

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part of the spinal tract, and it affords me great satisfaction to have independently arrived at the same result as that of Mr. Dwight, whose paper I did not see until towards the close of my work.

Of these, one proceeds from the lumbar, one from the thoracic, and one from the interscapulary region (this latter beginning to moult later: see Chart, Table VI.). In addition to these main centres, there is to be noted another for the portion to which I refer as "the Lower Neck Region" in the Chart. I have also pointed out the lateral rows as such, from which moult proceeds later, as a secondary feature.

I am also able to state that I had a similar notion about the agency of the blood-supply possibly influencing the early moulting conditions of these centres, as referred to by Dwight (*l. c.* p. 84), to which the specimen No. 12 testifies, and from which the present description of this tract is made, by having used a carmine injection for the purpose. In this I failed to procure the desired evidence, on account of some unsuspected internal injuries by shot.

From these main centres the moult spreads both forward and backward simultaneously, but slightly more in proportion in the latter direction. It shows signs of energetic progress nearly always in advance of any remiges, as shown in my earliest acquired specimens. It is also protracted during and often beyond the latest phases of development of flight-feathers, as specimens in which the moult of the latter is completed show. The middle row is in full vigour of new growth, and approaches completion much sooner than the time of appearance of primaries III.–IV., as shown on the Chart; the crown of the head, and notably the auricular regions (lores, &c.), being the latest of the lateral rows to change, except the sides of the nape.

The Humeral or Scapulary Tracts (Pterylæ humerales).

Pterylographically, this tract, which is a double one, has been defined by Nitzsch (37, p. 25) as being entirely divided by space (the lateral *Apteria spinale*) from the spinal tract previously considered. Although being more directly connected with the "inferior tract" by means of a band of closely-set rows of feathers, it is linked, nevertheless, in this particular species to the "spinal tract" by a contiguous set of softly-textured feathers consisting of about three rows. These are placed across the clavicular region in front of the head of the humerus, thus bisecting the long spinal apteria, a similar arrangement as that ascribed to some birds by Nitzsch (p. 25, *l. c.*), e. g. *Steganopodes*, *Buceros*, and *Colius*, which, as he remarks, "may nevertheless be recognized as distinct tracts by the stronger formation of their feathers."

The humeral tract may be subdivided into two distinct portions, each with a well-marked centre from which the moult spreads independently, a humeral and a clavicular, or more marginal portion, the latter merging into the alar marginal tract. Both these consist of several rows after their bifurcation. Of these, those medially situated are

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affected earliest, and simultaneously with the corresponding rows of the spinal tract; the internally and externally situated ones which compose these branches begin to moult somewhat later, about the same time as the renewal of primary remex III.; this is also the case with the lateral rows of the thoracic portion of the spinal tract. The moult for the feathers of this tract on this part of the body sets in most vigorously, and is achieved at a comparatively earlier period than that of the dorsal main stem.

Closely allied to the distal rows of its humeral branch are the feathers which compose the "Parapterum." Only a narrow space separates the two. The feathers of the latter take up the moult from the humeral branch, and in younger birds are replaced by synchronous appearance, whereas in older individuals they are renewed in more regular sequence from within outwards.

The more marginal branch spoken of, and entered also in Chart (Table VI.) as "clavicular," follows the same principle for the moult of its feathers as that which applied to the former branch. Its distally situated rows on the underside of the wing establish a connection with the "Hypopteron," from which it is but slightly separated also. The feathers of the Hypopteron, which are a somewhat rudimentary set (being of a filo-plumaceous structure), begin moult—which is always a simultaneous one for them—later than those of the Parapterum, their appearance corresponding with the renewal of primary V.

The Inferior or Ventral Tracts (Pterylæ gastræi).

Commencing with the chin, and covering the throat in one homogeneous mass, together with the head and sides of the neck, with which portions it coalesces, this tract divides itself into two stems in the gular region, which descend in a laterally-curved line towards the anal region, without, however, reaching the orifice. These two stems enclose the *apterium mesogastræum* of Nitzsch (p. 34, *l. c.*). Excepting the portion of the throat mentioned above, its rami may be further subdivided into "pectoral" and "inguinal" portions respectively. The former are of considerable width, and consist of about from eight to ten longitudinal rows of feathers in their broadest parts. These send off the lateral extensions, backward and outward, referred to by Nitzsch (*cf.* p. 27, *l. c.*) as *pterylæ laterales*, more prominently perhaps in the species under examination than in those Passerine forms referred to by the latter author (*cf.* pp. 28 & 80, *l. c.*). These small ramifications set off distinctly enough immediately in front of the portion which forms the greatest expanse in the double tract just below and posteriorly to the arm-pit.

At a place slightly in advance of the junction of the latter with the main pectoral portion is the principal centre from which the moult proceeds longitudinally backwards, and to both sides of the tract, by renewing every alternate feather, sometimes overlapping two feathers in either direction. The inner rows of this portion moult with great rapidity during the earliest stages of the complete feather-change; whilst

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EXPLANATION OF TABLE VI.

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In the 3 divisions above the *horizontal line*, which is extended to the left, are entered the flight-feathers of the *Alar tract* in the order of their moult from left to right.

The metacarpo-digital remiges or primaries for which the Roman figures I.–X. (XI.) have been substituted are placed in the *top portion* of the lower division and serve as the chronological scale by means of which the moult of all the other tracts with their component rows may be compared.

The *lettering* in the portion below this and immediately over the line corresponds with the lettering for the metacarpo-digitals in Tables I. & II. and Plates XXXVI.–XXXVIII.

The Roman figures in the *lower portion* of the *middle division* show the synchronous replacement of the cubital remiges or secondaries with any of the primaries in moult. They are lettered with dashes thus: ′, ″, ‴, in conformity with that of Tables I. & II. and in Plates XXXVI.–XXXVIII.

Above these and in the *uppermost division* in ordinary cyphers are placed, according to their order of replacement, the *Pennæ pollices*, synchronous in position of their moult with those of the respective remiges.

Each *shaded bar* represents the moult of the respective row or rows of feathers, denominated as such to the left of it.

Its *pointed end* indicates the commencement of the moult of the row of feathers which it represents.

The *tapered portion* of the *bars* from the tip to the angles which its sides form with the parallel divisions of horizontal lines, shows the comparative amount of moult for that row.

At the *place* where the *shading* fills up the parallel divisions, the moult of this row of feathers is completed.

By means of the *vertical division lines* their respective stages of moult may be read off on the scale provided for the moult of those remiges with which these stages coincide.

A × against a unit of rows or a particular row signifies that this is a particular centre from which moult proceeds.

The rows which constitute a tract are bracketed together and are headed by the pterylographic name of their respective position.

The latter are bracketed together again according to their anatomical position on the bird, and denominated as such at their head.

The *division* at the *foot* of the Table is devoted to the synchronism in moult for the *tail-feathers* by means of *bars* for the *coverts*, both dorsal and ventral, and by their respective numerals for *main quills* or rectrices.

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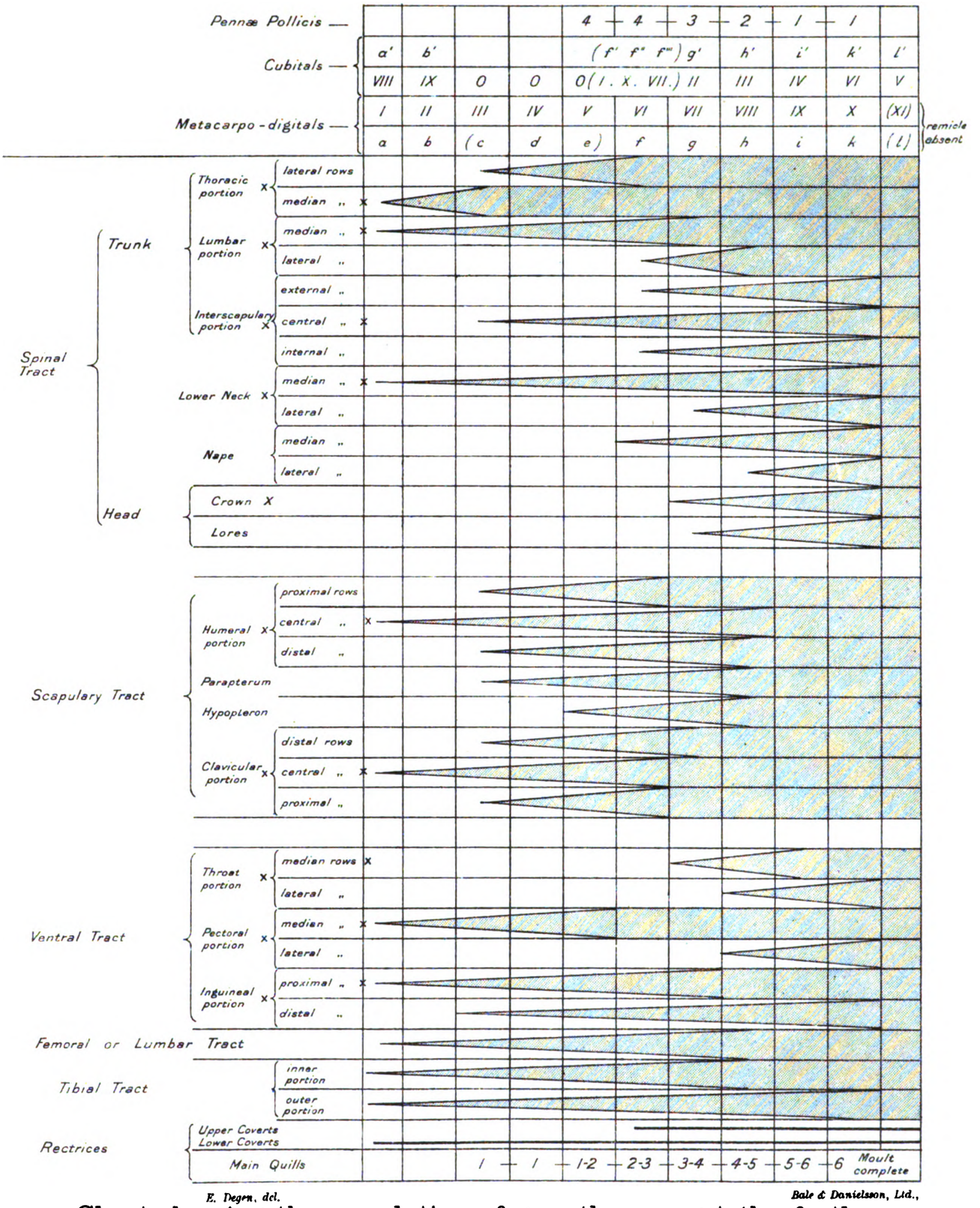
To face p. 898.

TABLE VI.



E. Degen, del. *Bale & Danielsson, Ltd.,*

Chart showing the correlation of growth amongst the feather tracts during the period of the moult.

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the lateral rows, both internal and external ones—to which latter the pterylæ laterales belong,—do not take up the change until considerably later, viz. the stage of renewal of primary remex VIII.

The centre of moult from the other, namely, that of the "inguinal" or gastric portion—which is a continuation of the pectoral one, consisting of three or four rows of feathers only,—begins also synchronously with that of remex I., or directly after. The progress of renewal of the feathers of this portion is much slower, though slightly faster in the case of the innermost rows than the lateral ones. This condition points to the fact that the inner rows are really equivalent to the median ones of an undivided tract.

The third centre of feather-renewal for this tract is at the point of bifurcation for the two pectoral *rami* on the lower throat. Contrary to the mode of moulting, in an antero-posterior direction, of these latter, the moult of this portion proceeds in a forward direction only, until it finally reaches the *mentum*. It is not till much later on in the season of general moult that it sets in here; but when it does, it happens in a vigorous manner, which is about the time of remiges VI. and VII. for the central rows. These are followed immediately by the outer rows, which complete their moult at the time of renewal of cubital remex V., the last of the flight-feathers to moult.

The renewal of the feathers of this tract in the order in which it has been described here is that of the older individuals. In younger birds this order is not so clearly defined.

The Femoral or Lumbar Tracts (Pterylæ femorales *seu* lumbales).

These are composed of two rows, consisting of nine or ten soft and elongated contour-feathers each. They are renewed in alternate rotation—that is, by beginning in the superior row with the feather which is situated nearest the *apterium spinale*, to be followed by that of the inferior row next to it, and from whence the feathers are renewed in tolerably regular sequence in backward direction. Though the feathers of this double tract are only few, their renewal, which begins with the earliest phases of the flight-feathers, is not completed till about that of remex VIII.

The Crural or Tibial Tracts (Pterylæ crurales).

Both portions of these tracts, which clothe the tibia—an inner and an outer one—and which are separated in their upper or femoral portion by an apterium, merging with each other below the knee, moult simultaneously. The moult begins early and synchronously with the centre of moult of the other tracts, from above below, and finishes on the tarsal joints. The time of completion corresponds with the last stages of flight-feather renewal. This is somewhat remarkable for a tract which consists of so few feathers, seeing that their renewal begins at a comparatively early period of the perennial moult and finishes so very late.

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The Rectrices and their Coverts.

The tail-feathers are replaced in a perfectly regular order from within outwards, as are also their coverts, both dorsal and ventral. These coverts consist of two rows each, equivalent to the major and the median coverts of the remiges.

The first or innermost pair of rectrices—of which it is sometimes the left, or as in some individuals the right side, which moults first—is renewed at the time of renewal of primary remiges III., IV., and V., or the triplet marked *c*, *d*, *e* (see also diagram, Plate XXXVI., and Tables I. & VI.), as has been pointed out.

About the time of renewal of the 5th primary, the second innermost pair of rectrices takes up the moult, generally before the first is completed, and, with the next remex in moult (viz. primary VI.), the third pair follows suit, and so on; the last and outermost sixth pair coincides generally with the two outermost metacarpo-digital remiges IX. and X.

Frequently there are as many as three pairs of tail-feathers to be seen in various stages of graduated length of renewal, but, as a rule, there are not more than two. The former condition occurs in younger, whilst the latter is the case for older individuals. Their dorsal coverts take up the moult somewhat later than their ventral ones, which latter are amongst the first feathers to renew of the whole plumage, as may be seen, by their relative order to the rectrices, at the bottom of the Chart (Table VI.).

IX.—Conclusions.

Having, in the preceding pages, described the chronological behaviour of the feathers during the moult of the individual, and further shown, with the help of diagrams and tables, the relationship of their development to one another, by paying special attention to the principal feathers, I can now proceed with the explanation of my views with regard to the manner in which they reflect the phylogenetic conditions of the archæornithic type from which the wing of the modern bird has been evolved. For this purpose it becomes inevitable to refer again to the details of the theory propounded in the pages of my former work (16) and notably so to plate i. fig. 3, *l. c.*, for the views there brought forward.

The present investigation gives me no cause for materially altering the fundamental plan laid down in the former paper, other than two slight modifications. The first and principal one, referred to already under the part headed "Ala spuria," is the result of the additional discovery of the inverse order in the shedding and eventual replacement of the *pennæ alares* of this portion, as affording us a *likely key* to its further solution. The other point is one of a merely subordinate character, and I propose to allude to it later on.

Immediately on entering upon the question, our attention once more gets directed

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towards that point which forms the focus in the whole problem, viz. the *diastema*, for the position of the 5th cubital remex. The space between the first primary remex on the metacarpus and the sixth secondary one is occupied by cubital remiges I.–V. (exclusive of a carpal vestigial one), with their respective main coverts, which form the most distal group on the forearm, and here spoken of as Group II., on account of the moulting of these feathers second in order, and therefore in keeping with this particular feature.

All the members of this group moult in inverse order, viz. from the wrist-joint inwards. To these, in my former diagram (pl. i. fig. 3, *l. c.*) of the reconstructed wing, was allotted a metacarpal position; and, in allusion to their possibly former digital derivation, they were referred to as "proto-metacarpo-digitals."

The significance of a similar fact of the "*pennæ pollicis*" moulting in an inverse direction, too, assumes now additional importance through this peculiarity. As mentioned before (p. 371; see "Ala spuria"), that it probably would matter little whether these feathers were regarded from a purely remigial or a tectricial point of view; this again finds corroboration in this place, since main coverts follow the same routine order of moult as do remiges. But what really transpires is (especially when taken in conjunction with the sectional moulting of the flight-feathers on the manus, as in the Kingfishers and others, and further shown for the dorsal median coverts in this species) that we have clear testimony in this of the presence of a distinct *digital*, and an equally distinct *metacarpal*, element. To the remiges of the former derivation therefore alone belongs the term *proto-*, whilst to the latter belongs that of *hypo-metacarpo-digitals.*

If then, as the principle of analogy would justify us in adopting, the same rule by which the remiges of the former Group II. (and now become our *Hypo-metacarpo-digitals*, or further abbreviated "*Metacarpals*") were applied to our permanent meta-carpo-digitals I.–X. (XI.) (or frequently more as in the Ostrich and probably in the archæornithic wing), the only possible inference would be that these latter are those of purely *digital* origin.

As such then, and the fact that both sections of which the series is made up, viz. from I.–VI., and the other from VII.–X. (XI.) and moulting both in an outward direction, it is these which now become our true "Proto-metacarpo-digitals" of the hypothetical wing.

In the "modern wing" those of the outer section alone, namely, primary remiges (VII.?) VI.–X. (or XI.), deserve henceforth the appellation of "Permanent Digitals" (see former diagram). On the other hand, the primaries of the inner section, viz. I.–VI. (having, in association with synostosis of the metacarpal bones belonging to digits II. and III., been borrowed from their previous phalangeal position on digit III. by the now combined metacarpal bones with which they have become

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permanently associated) deserve to be called "permanent" only in so far as they are derived from the same source as the former.

All that remains to be further explained now, after having shown their purely digital value, are those *digital phalanges* on which they were originally situated. These could have been none other than those belonging to digit III., as we shall see.

The crowding together on the wrist of the flight-feathers in their backward-shifting process towards the elbow caused the forearm to receive first the quills originally belonging to digit IV. Next to these followed the "metacarpals" belonging to digit III. This must have occurred contemporaneously with the process of ankylosis of the two metacarpal bones, so that these "digital" remiges in question and belonging to digit III. found the channel obstructed by their former neighbours, the "metacarpals" mentioned above, which had preceded them in this course of shifting into their new position on the forearm and in the latter of which they became fixed. Hence, in the same manner, they became fixed themselves, in turn, on the combined metacarpal bones.

Another peculiarity which has often arrested my attention also seems to point strongly to such a rearrangement. It is that of primary digital remex VII., or, anatomically speaking, the "addigital," which, instead of having its base inserted, like those of VIII., IX., X., or XI., on the phalanges which bear them, crosses the retained terminal phalanx of digit III. entirely, to insert itself above it, together with the shafts of all those from this one inwards, on the metacarpal bone of digit II. This arrangement is also distinctly shown in Wray's (46) text-figure on p. 351 (fig. 2 *a*, *l. c.*) for the faithful drawing of the wing of an adult Ostrich, in which bird, owing to the greater relative length of this complex terminal phalanx, the shafts of no fewer than three primaries likewise cross it.

A reference also to my former diagram (table i. fig. 3, *l. c.*) shows that in this I suggested, by means of dotted outlines, a suppositional remex to have been present, as well as that of the "carpal remex and its covert"; it is marked there I′, and × on phalanx I. of digit III. When this digit was probably slightly inferior in length to digit II., but otherwise composed of the same number of phalanges (see also Wray, (45), p. 284, "Note on the Vestigial Structure in an Adult Ostrich," figs. 1–4 representing the digital phalanges of digit III.), it was doubtlessly capable of giving accommodation to a similar number of remiges like that composing the inner section of the primaries, as in the present forms of birds. In fact, Wray shows this number to be equal for the Ostrich, namely 8 "metacarpals" and 8 "digitals."

The next point of difference to account for concerns those flight-feathers on the cubitus which compose Group III., the last to moult, and comprising secondaries VII., VI., and V. In my former drawing the metacarpal bone of digit IV. is represented as carrying one remex only, namely cubital VIII.

Having seen that IX. and X. also moult in an inward direction, the inference from

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this would be that this bone was probably the carrier of more than that remex VIII. by further including IX. and X. also.

Inferentially, from their outward order of moult, both VII. and VI. being of digital origin, their position on the first phalanx of digit IV. would require no other alteration to my former diagram, except perhaps the cubital remex V.—which, according to its moult, seems to belong to the set of flight-feathers composing Group III. (further shown in the scheme on p. 404)—takes up the outermost digital position of digit IV. instead of the most inward metacarpal one to which I then assigned it.

For exactly the same reasons "carpal remex and covert" become "last metacarpals" of digit III., instead of being, as interpreted previously, "first digitals" of the same finger. It is merely a shifting backward by one place *in toto*, with the further consequence that "cubital remex V." of the specialized Passerine forms requires to be also theoretically included with the remiges (0 carpal remex) I.–IV., our present Group II. and the most distal on the forearm, by means of this disposition.

Indeed, the greatly vacillating position in the order of its renewal which this flight-feather takes up makes it difficult to determine whether it moults last of Group II. or first of Group III. It seems from four specimens (Nos. 24–27 of diagrams, Plate XXXVIII., left and right wings) that it is connected directly by moult with the remiges of the distal group in Nos. 25 and 26; whilst in No. 24 it holds a position strictly intermediate, the new-growth remiges IV. and VI. in the two wings of this specimen having been fully accomplished. Its determination as to new or old growth in specimen 27 being somewhat doubtful (see Table I. parts *a* & *b*, and also diagrams K, L, M of Plate XXXVIII.), the latter gives no positive information on this point.

This slight preponderance in favour of its closer association with the distal group is fully counterbalanced by the opposite condition of moult of this remex in specimens 28 and 29, which were both received on a later date, namely March 20, and preserved in a dried condition on account of their almost completely finished moult. But the following notes on these, taken down when fresh, will confirm the above:—

"No. 28, ad. ♀, March 20.

"Remarkable specimen on account of its white back (albinism or hybrid between *G. tibicen* and *G. leuconota*?).

"Moult complete *with traces of same on wings* (both sides) *for cubitals* V. *and* VI. Incomplete on dorsal tract."

And for:—

"No. 29, juv. ♀, March 20.

"The 6*th cubital* of the *right-side wing a little shorter* than *corresponding feather of left*. The 5*th* cubital apparently the old remex not yet shed."

By preferring the incorporation of cubital remex V. of the Passerine type of bird with the distad group, we necessarily encroach upon the number of remiges of the middle group, viz. V., VI., & VII., which in this case would reduce this group to only

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two quills, namely VI. & VII. Naturally, then, this would restore to the distal group the number of remiges allotted to them in my former diagram. And, in continuing this process of borrowing one remex from group to group backwards consistently, it certainly would have the advantage of bringing us in positive accord with the results arrived at in the compilation of my former diagram, namely by ending with secondary remex VIII.; thus leaving us with remiges IX.-X. to be disposed of as "remiges cubitalis veri."

But against the inclusion of cubital VIII. in the middle group is seen *the perfect constancy with which the latter remex begins the moult first in all the specimens*, to be followed in turn and with equal constancy by secondary remex IX. It is not till much later in the moulting-season that in Passerine species remex VII. begins its renewal, in fact not before VIII., IX., & X. are all nearly completely renewed.

The fortunate acquisition of the two wings of a Moor-hen (*Gallinula chloropus*) in just such a stage of moult, as well as numerous material of Parrots in the same condition (notwithstanding the fact that the former belongs to a eutaxic family of birds), shows that in these birds (a fact in which they all agree) *it invariably is the cubital remex* IX. with which their moult begins first on this portion of the wing.

Moreover, an examination by Pycraft (39) fig. 4, pl. 14, of the wing of a young fowl, convinces me that the "eutaxy" of the Gallinæ—and probably all those more primitive groups of birds which compose Mr. Pycraft's list of eutaxic forms (see p. 248, *l. c.*)—is morphologically not the same "eutaxy" as that of the Passeres.

The constancy with which in diastataxic wings moult sets in first with cubital remex IX., by commencing the renewal in an inward direction of the proximal Group I., against the commencement in the latter with remex VIII. of the Passerine mode, legitimately points to the assumption that these two quills are morphologically identical with one another, and that the cubital remex V., where it is present in such eutaxic forms as the Gallinæ and similar birds other than Passerinæ, is the original remex V. still retained by them.

The following scheme will further express my meaning:—

Scheme for right side of Wings.

	Group II.						Group III.			Group I.
Galline eutaxy	(0)	1	2	3	4	5	6	7	8	9——*x*.
Numerical figures of cubital remiges	(Carp. R.)	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.——*x*.
Passerine eutaxy.....	(0)	1	2	3	4	0	5	6	7	8 9 10 (11)
	Group II.						Group III.			Group I.

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Whether cubital remex V. in the Passerine type of eutaxy is really a member of the distal or of the middle group cannot be determined positively by means of the present material; but it will in all probability be found to belong to the latter, seeing that it takes up the moult more frequently from the 6th and not from the 4th. This is only what may be reasonably expected from a flight-feather which is actually remex VI., and numerically only remex V., as in the present species. Of the original remex V. in the Galline type of eutaxy, there is not much doubt as to its belonging to the distal group.

It has been suggested (see *anteà*, p. 401) that the inner section of metacarpo-digitals, at present situated on the combined metacarpal bones—on account of their eminently "digital" character,—were elements originally belonging to the digital phalanges of digit III. Since we have found in our former "*proto-metacarpal digitals*" (cubital group II.) *the true original metacarpal elements* belonging to the metacarpal bone of the latter digit, we see that this distribution leaves us minus a similar equivalent for the metacarpal bone of digit II.

From this the question arises as to what has become of this series, or are they really anywhere at all?

The answer to it is not so obscure, and is one to which Goodchild, Wray, and Pycraft have contributed.

The survivors of this set of feathers are present still in the diastataxic wing, and the older forms of the eutaxic birds, in the shape of that enigma of a part-series, which is situated on the distal portion of the forearm known as the "intercalary row." In the majority of those birds this row consists of from 5–6 feathers, but their number is reduced to 4 in some. If they are not actually the aborted flight-feathers themselves (as I suspect them to be, from the fact that in the specimen of a young Parrot—*vide* text-figure 2, p. 364,—contrary to the presence of sessile neossoptiles for all the other covert-feathers, the latter are, curiously enough, absent on both sides) they are at least the major coverts of the entirely suppressed remiges to which they belonged, and which are the set of feathers to be yet accounted for.

This latter supposition would constitute a case of "apoptilism" for the whole series, the same as applies to that of the *Parapterum* (Degen, 16). Of their pterylo-genetic relationship to the other covert-series on the dorsum, I would refer to Goodchild (27), in whose drawings they are marked by the letter C. Goodchild has found them to be such excellent landmarks for the determination of the rows that the following quotation from his paper gives a sufficient idea as to their value for further collateral evidence. This is what he says on p. 189, *l. c.*:—

"In the type of wing-feathers prevailing throughout all, or nearly all, the rest of the Psittacidæ (in speaking of an additional row of backward-lapping wing-feathers in *Melopsittacus*) an additional modification may be observed. The row of feathers

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coming on next above the greater coverts, indicated by the letter C (*intercalary row*) in the following diagram, is seen to consist of a series numbering generally five or six, which are confined to the distal areas of the cubital region, and form a distinct and separate series from the feathers that extend across the median area. *They correspond in relative position to the upper wing-coverts* (t.m.) *in the manual region of the wing*" [1], &c. And further on :—"The feathers referred to often form a conspicuous feature on the wing of the living bird, as they are frequently arranged in such a manner that the shafts of three or more of the feathers are in a line. *The proximal edges of the feathers are generally as firm as those on the opposite side* [1], and, as a consequence, the whole series slides between the feathers next them on the proximal side in much the same way as the blade of a lancet closes in its sheath," &c.

Wray (46) also drew attention to this set of feathers, and after rectifying in his paper a few incongruities which arose out of Goodchild's nomenclature for the grouping of portions of the series on the wrist, dismisses the subject (p. 350, *l. c.*) with the following remark :—

" Grouping the feathers according to their insertion, and remembering the conditions of folding which must occur on the wrist, the observations of Goodchild give the most complete view of this subject we have."

It is in Pycraft's excellent thesis (39) that the greatest amount of significance as yet attached to the presence—better expressed *appearance*—of this set of flight-feathers called the " intercalary row " has been most signally pointed out. But how much the introduction of this element became responsible in the " shifting process " (chiefly transverse) of all the rows of the distal portion on the forearm, with its consequent " faulting," a glance at the drawing of his own preparation, of the nestling *Lomvia troile* (*cf.* fig. 2, p. 243, *l. c.*), suffices to show. He thus lucidly describes it :—

" The disturbance is much more obvious in the row of papillæ immediately above the remiges—the rudimentary major coverts 1–5. These have become distinctly separated from the rest of the row proximad of this point. The disturbance of the rows preaxial to this of the major coverts is barely perceptible. *There is yet no intercalary row* " [1].

Why, in spite of the impendingly disturbing influence they exert at this critical stage, he never so much as attributed to them *the real cause* of the general disturbance which his later stage (of the above figure mentioned) so clearly demonstrates, seems incomprehensible now, although clearly capable of explanation. The reason is that he connected them—upon their sudden appearance—embryo-genetically with the members of the rows of either the Medians, or those above the latter, *e. g.* the Minors, entertaining even some slight doubts about their serial value as regards the latter's first or second row; instead of treating them as the real cause which separates the

[1] These *italics* are mine.

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Medians from the Minors between which they wedge themselves in. With regard to the unsteady location of this intercalary row, in describing on p. 242 (*l. c.*) the two different stages of the wing of a Lapwing (*Vanellus cristatus*, pl. 14. figs. 1 & 2) he says:—"It is of interest to note that the downward shifting in this case must have been but slight, *as the intercalary is the 2nd and not the 3rd row of coverts*[1], as was the case in the typical wing described on p. 239."

That there is still another peculiarity which attaches to this row seems almost a possibility, though not sufficiently clear as yet. It is that their position as regards the Parrots is undoubtedly immediately above the major coverts; this is confirmed by Goodchild; whereas, to judge from Pycraft's well-executed drawing of the wing of the young fowl and that of the *Lomvia troile*, they are unmistakably placed above the medians. I have no doubt about this interpretation as being correct also. But it seems to suggest one thing, and that is, that they originally wedged themselves in between different rows in different groups of birds, sometimes above, sometimes below the medians.

Their appearance takes place at a time when both the wing-membrane and the bones are still very plastic. While in this condition, the contact of the flight-feathers with the latter is much less intimate as far back as the region of cubital V., to which point hardly any impressions of the contact of the remiges with the ulna can be found. It is only proximally from this point that the bone shows traces of their contact in the shape of sockets consisting of pits and tubercles, which are retained throughout all the moults, and which are the outcome of the early fixtures of the remiges on the posterior portion of the ulna.

If the feathers composing the group of intercalaries were derived from the minor series, the order of their renewal should correspond with these latter, which is an outward one. Such, however, is not the case, as seen in a specimen of a Parrakeet (*Platycercus eximius*) in my collection, and dated from March 4, which shows this particular stage of moult. In this the renewal proceeds in the same inward direction as do the flight-feathers, their major and median coverts,—all belonging to the distal group. On its right-side wing the 3rd, 4th, and 5th, or most proximally situated feathers of this intercalary row, are to be seen in successive stages of growth in the numerical order quoted; whilst the 2nd and 1st respectively, or more distal ones, show unmistakable signs of their having quite recently attained full development. On the wing of the other side, this stage of moult is slightly more in advance, the 6th or last feather being in process of renewal only.

A specimen of a Musk Lorrikeet (*Glossopsittacus concinnus*) also shows the same arrangement. In consequence of this fact, the significance of flight-feathers as an additional integer requires to be placed upon this set of feathers, similar to the

[1] These *italics* are mine.

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remiges I.–IV., with the further definition, however, of a former "metacarpal" derivation.

The following scheme will be found to supplement the original distribution of the flight-feather elements on the fore limb of the ancestral bird, according to the evidence adduced in its favour through this work. It represents the left-side wing.

Revised Scheme for the Derivation of the Flight-feathers from the Tetradactyle Ancestral Form of Birds.

Proto-metacarpo-digitals = Flight-feathers of Phalangeal Origin.	*Hypo-metacarpo-digitals* = Flight-feathers of Metacarpal Origin.
	Digit I.
Suppressed (lost).	Present Pennæ pollicis IV.–I.
	Digit II.
Present Metacarpo-digitals XI.–VI.	Present Intercalary row I.–VI.
	Digit III.
Present Metacarpo-digitals V.–I.	Present Cubital Group II., Secondary Remiges (0) I–IV.
	Digit IV.
Present Cubital Group III., Secondary Remiges V.–VII.	Present Cubital Group I., Secondary Remiges VIII.–X. —Cubiti veri XI.–*x*.

Direction of Moult.

From the foregoing scheme it may be observed that there are no flight-feather equivalents allotted to the phalangeal portion of Digit I., in which part they figure as "suppressed."

Such a condition is quite conceivable and in perfect accord with suppression of quills in other portions, as, for instance, the reduction on the extreme phalanx of the second finger from 12 to 11 (Podicepidæ, Pelargi, &c.), and from 11 to 10 and 9 in Passeres (Gadow, 21, pp. 656 &c.). This tendency towards a part-suppression, if carried further, would have the effect of leading to total apoptilism. It, moreover, must have proceeded contemporaneously with the feathering of the forearm and was still in progress after, as is evidenced in the Passeres, where it has reached the present climax in the Oscines proper.

Considering the genealogical relative shortness of Digit I., coupled with the fact of a still greater reduction of size in the present forms of birds to one compound element, there is a strong probability existing that, during the course of the fusion of the phalangeal segments of this digit with its originally independent metacarpal bone,

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they were stripped off one after the other as in the case of the "Remicle" and other diminutive terminal coverts. A likely procedure for feathers which at no time could have been of any considerable size, and certainly not more in number than three at the most.

The moult of the "Pennæ pollicis," moreover, synchronizing with that of Metacarpo-digitals VI.–X. and Cubitals I.–IV. (see Table VI.), is by no means an unimportant item for the argument that in their retrograde movement they were obstructed by the position which these latter, together with the "intercalaries" (as representing the metacarpal equivalents for Digit II.), had early taken up on the distal portion of the cubitus.

Finally, if the present inquiry into the moult of the individual bird, which, however, reflects all the phylogenetic conditions inherent to the Class as a whole (except perhaps the Spheniscidæ), has not thrown any further light upon the question as to whether "diastataxy" is due to either the hypothetical *absence* of a remex or the assumed *presence*, consequent upon the "shifting" process alone, as summarized by Pycraft (in his paragraph (1) p. 241, *l. c.*), it should at least have contributed materially towards the outstanding answer of the first part of the latter author's paragraph (3)—"The cause of this shifting is still a matter for investigation"; and also to the second part of the same sentence—"it is possibly due to a slight secondary lengthening of the forearm."

This latter interpretation does not seem to gather strength, especially when we perceive the ample manner in which the "moult" supplies the proof that "faulting" is not confined alone to diastataxic wings, but takes place, though in inferior degree, in the short-armed eutaxic forms of birds, such as the Passeres.

My sincere thanks are due to the following gentlemen:—

To Mr. J. Orme, of the Victorian Railways, Murchison East, Victoria, Australia, who by his disinterestedness in supplying me with the specimens has so materially aided me in my task.

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Also to the Staff of the Society's Library and the Publication Department, for the ever-courteous manner in which my wants were met.

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XI.—EXPLANATION OF PLATES XXXVI.–XXXVIII.

The Roman figures placed at the head of each diagram denote the numerical order of the flight-feathers, as counted from the wrist-joint, outwards for the digital portion, inwards for the cubital portion of the left and right wing respectively.

The broader dark vertical bars indicate those remiges which are in progress of moult.

The symbol 0, placed over the bar indicated by dots only, signifies this particular remex is shed off.

The numbers placed immediately above the bars express the actual length of growth of the remex represented by that bar, in millimetres.

The proportionate growth of the remiges in moult may be read off on the scale from 0–100 (100 standing for full growth), which is provided for each diagram.

The small letters beneath each diagram indicate the chronological appearance of the remiges on the two portions of the wing—plain letters for the metacarpo-digital; with a dash, thus ′, for the cubital portion.

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PLATE XXXVI.

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PLATE XXXVI.

DIAGRAM A. Showing moult of metacarpo-digital remiges I. and II., or *a* and *b*, also their corresponding equivalents VIII. and IX., or *a'*, *b'*, on the cubital portion.

DIAGRAM B. Illustrates the anomalous case peculiar to the moult of metacarpo-digitals III., IV., and V., or *c*, *d*, and *e*, a triplet of remiges which has no corresponding equivalent on the cubital portion at this stage of development.

DIAGRAM C. Stage of development of previous diagram in a more advanced condition of moult, besides which remex VI. or *f*, or the next in turn, is shown.

On the cubital portion of the left side are seen also the remiges I., X., and VII., lettered f', f'', and f''' respectively, the triplet of flight-feathers which restores the temporary asymmetry formed by *c*, *d*, and *e* on the hand-portion, as shown in diagram B.

DIAGRAM D. Showing moult of metacarpo-digital VII., or *g*. The moult of its corresponding remex II., or *g'*, is indicated at this stage by being shed off. This stage forms one of transition between f, f', f'', f''' to that of g, g'.

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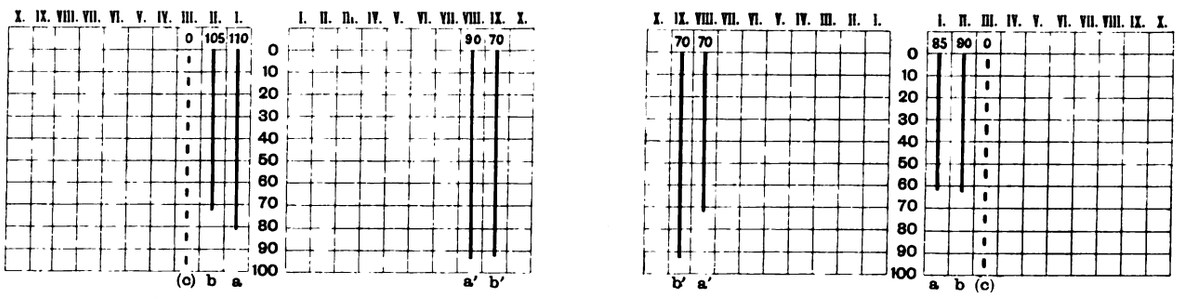
Left Side Wing. Right Side Wing.

SPECIMEN No. 1. ad. ♂ Nov. 5.

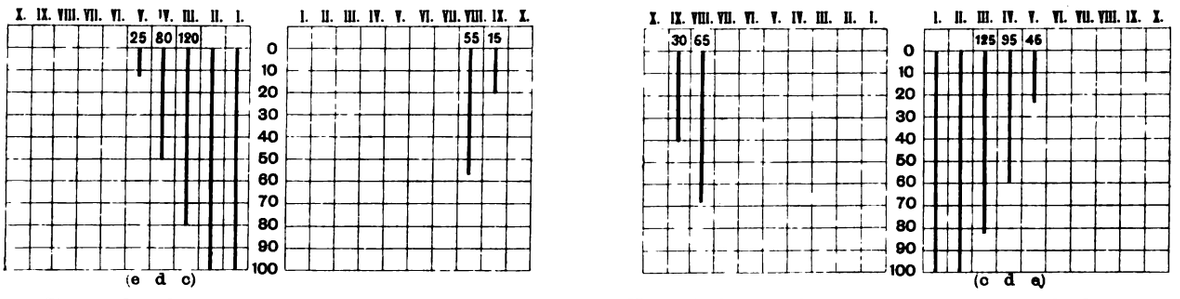
A



Stage of a and b, and a', b'. Stage of a, b, and a', b'.

SPECIMEN No. 3. juv. ♀ Nov. 14.

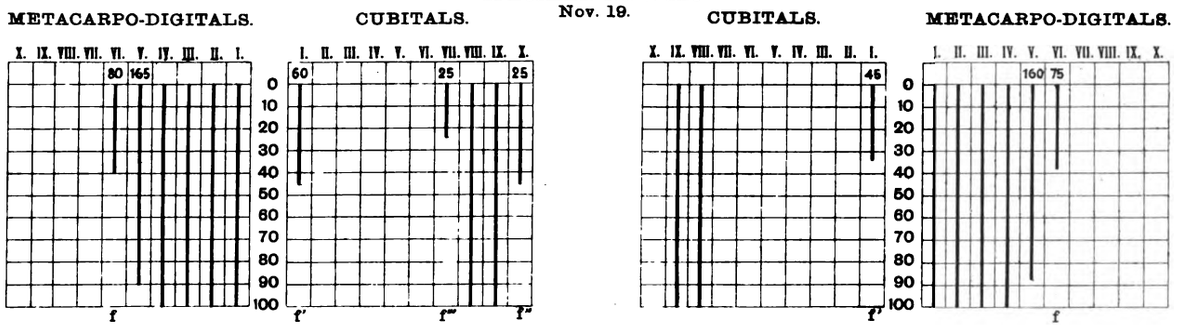
B



Stage c, d, and e. (No equivalent on this portion.) (No equivalent on this portion.) Stage of c, d, e.

SPECIMEN No. 7. ad. ♂ Nov. 19.

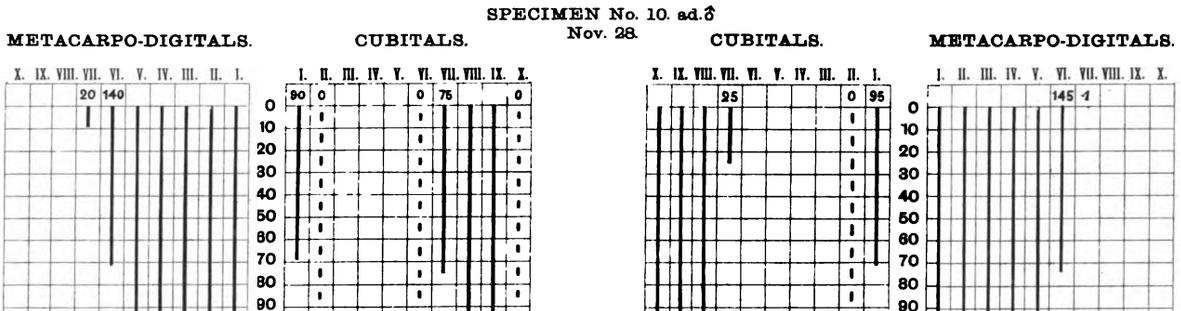
C



Stage of f, and f', f'', f'''. (imperfect for f'' and f''' see left side wing.) Stage of f, f'.

SPECIMEN No. 10. ad. ♂ Nov. 28.

D


METACARPO-DIGITALS.
CUBITALS.
CUBITALS.
METACARPO-DIGITALS.
X. IX. VIII. VII. VI. V. IV. III. II. I.
I. II. III. IV. V. VI. VII. VIII. IX. X.
20 140
90 0 0 75 0
25 0 95
145 4
0 10 20 30 40 50 60 70 80 90 100
g f
f' (g') (k) (f''') (f'')
f'' f''' (g') f'
f g

Stage in transition for f, f', f'', f''' and g, g'. Stage of f, f', f'' and f'''. Transition to g and (g').

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DIAGRAMS ILLUSTRATING THE MOULT OF THE REMIGES IN GYMNORHINA TIBICEN.

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PLATE XXXVII.

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PLATE XXXVII.

DIAGRAM E. Stage for moult of metacarpo-digital VII., or *g*, and cubital remex II., or *g'*, repeated. Here the conditions are reversed to those of diagram D. In this specimen it is the hand-portion which is in arrear, while the cubital portion is in advance.

DIAGRAM F. Intermediate phase of moult for metacarpo-digital remex VIII., or *h* (in arrear on both wings in this specimen), and its equivalent on the cubital portion remex III., or *h'*. This forms a case of transition from *g* to *h*.

DIAGRAM G. Showing stage of moult for *h*, hand-portion, and *h'*, cubital portion, in perfectly normal condition. Also early indication for the moult of metacarpo-digital IX., or *i*, the next stage, on the left-side wing.

DIAGRAM H. Shows the moult for metacarpo-digital remex IX., or *i* (abnormally in arrear in this specimen), and its equivalent remex IV., or *i'*, on the cubitus. Stage of transition from *h* to *i*.

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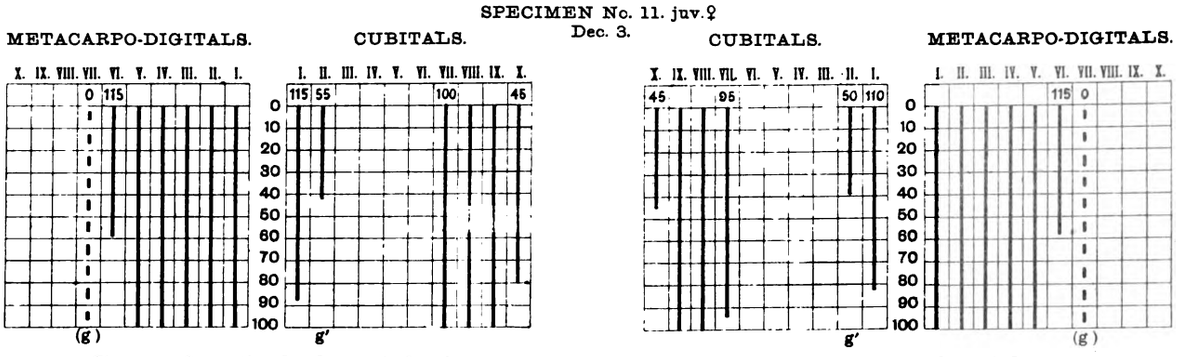
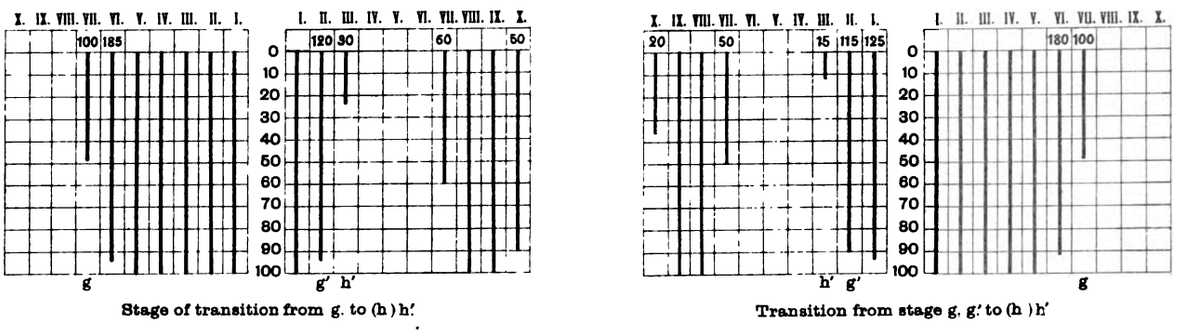
Left Side Wing. Right Side Wing.

E SPECIMEN No. 11. juv.♀ Dec. 3.



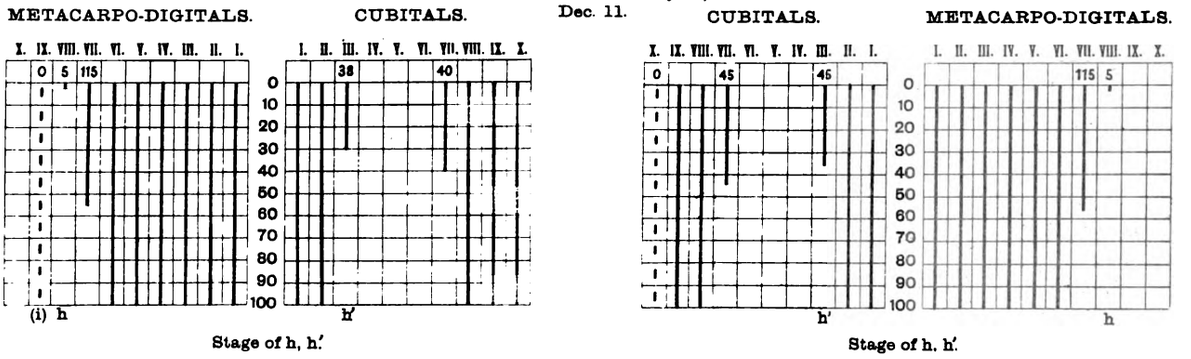
Stage supplementing development of g, g'. Stage of g, g' supplemented.

F SPECIMEN No. 16. juv.♂ Dec. 19.



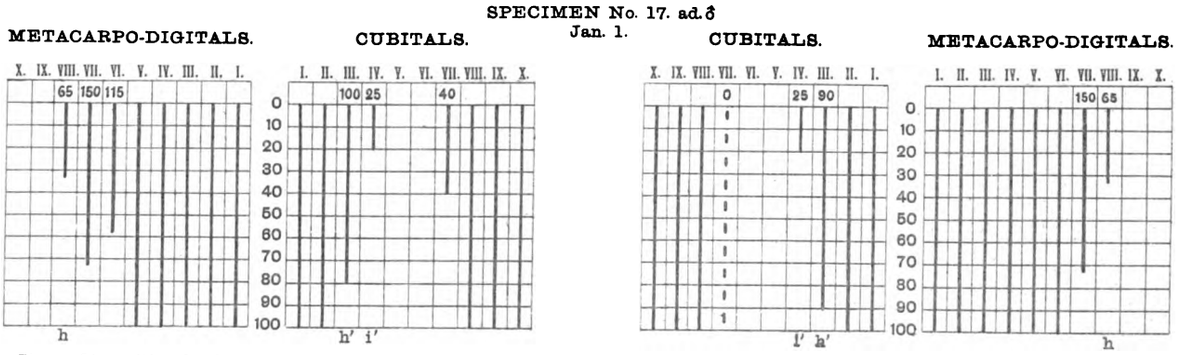
Stage of transition from g. to (h) h'. Transition from stage g, g' to (h) h'

G SPECIMEN No. 14. juv.♀ Dec. 11.



Stage of h, h'. Stage of h, h'.

H SPECIMEN No. 17. ad.♂ Jan. 1.



Stage of transition for development of h. h' and (i) in part i'. Transition from stage h, h', to (i) i.'

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DIAGRAMS ILLUSTRATING THE MOULT OF THE REMIGES IN GYMNORHINA TIBICEN.

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PLATE XXXVIII.

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PLATE XXXVIII.

DIAGRAM J. Moult of remex IX., or *i*, on the hand-portion, and its corresponding remex IV. for the cubital portion, in a perfectly normal condition for the left-side, imperfect for the right-side wing.

DIAGRAM K. Represents the stage for the development of metacarpo-digital X., or *k*, and that of its equivalent for the cubital remex VI., or *k'*.

DIAGRAM L. Shows the final stage of the moult for the flight-feathers, or that of cubital remex V., and lettered *l'*, which under normal conditions finds no equivalent on the hand-portion. It further supplements stage *k*, *k'* for the left-side wing only, being in arrear of moult for these on the right side.

DIAGRAM M. Specimen in arrear for the moult of metacarpo-digital X. on both sides, but otherwise showing final stage, or that of cubital V., to advantage.

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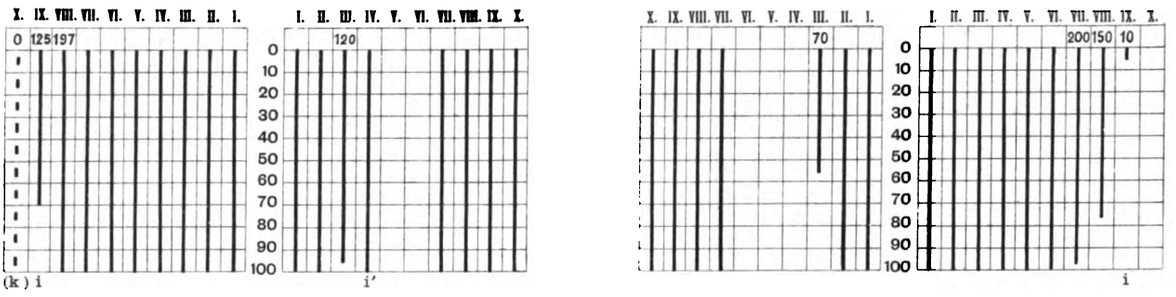
Left Side Wing. **Right Side Wing.**

SPECIMEN No. 21. ad. ♂
Jan. 29.

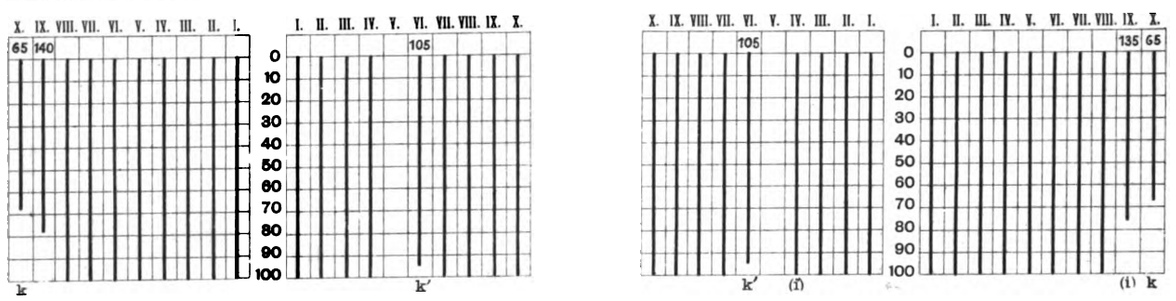
J



Stage of i and i'. Stage of i (imperfect for i')

SPECIMEN No. 25. ad. ♂
Feb 18.

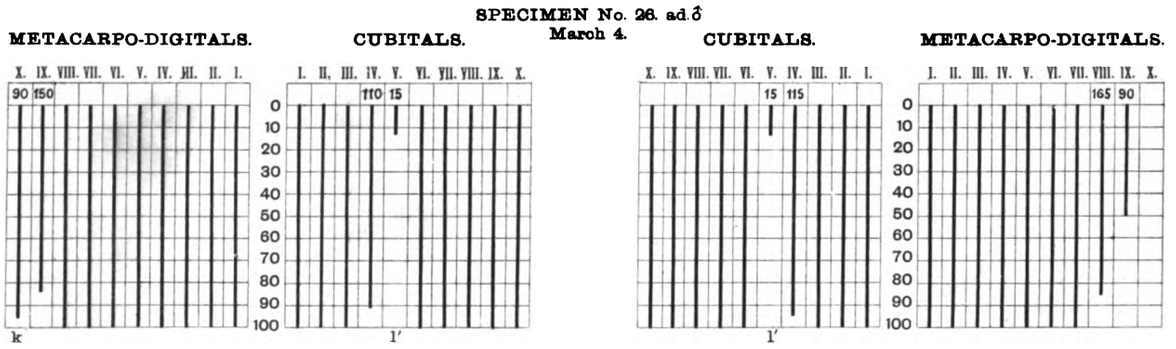
K



Stage of k and k'. Stage of k, k'.

SPECIMEN No. 26. ad. ♂
March 4.

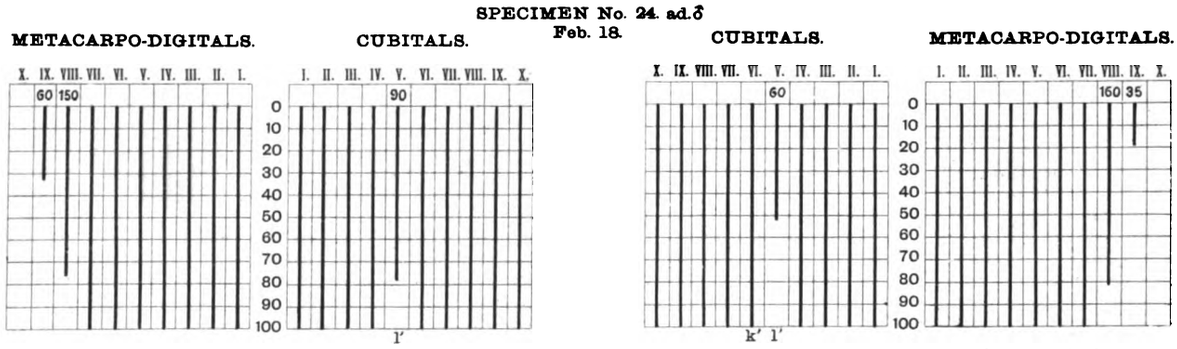
L



Stage of l' (no equivalent on hand portion). Stage of l' (no equivalent on hand portion).

SPECIMEN No. 24. ad. ♂
Feb. 18.

M



Supplementary stage of l' (final development) spec. in arrear for k. complete for k'. Stage of l' (further development) in arrear for k complete for k'.

E Degen. del

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DIAGRAMS ILLUSTRATING THE MOULT OF THE REMIGES IN GYMNORHINA TIBICEN.

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